

COMMONWEALTH BUREAU OF HELMINTHOLOGY,

THE WHITE HOUSE,

100, ST. PETER'S STREET,

ST. ALBANS, HERTS.

The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

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Vol. 65, 1961

(January, April)

PUBLISHED BY THE UNIVERSITY OF NOTRE DAME
NOTRE DAME, INDIANA

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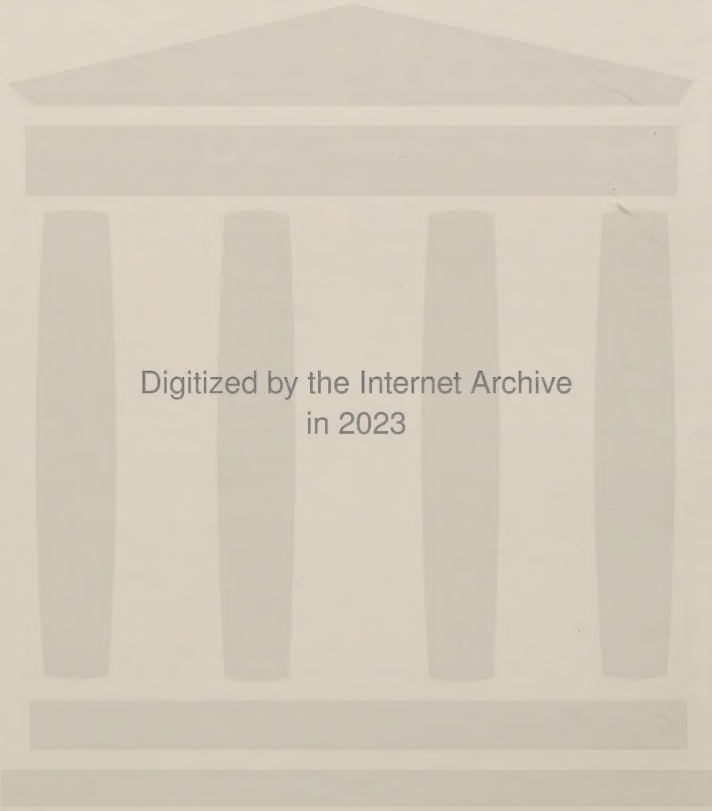
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The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 65

JANUARY, 1961

No. 1

Additional Remarks on the Evolution of Trunk Musculature in Snakes

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ABSTRACT: Certain of the more important aspects of the epaxial trunk musculature of *Xenopeltis*, *Eryx*, *Calabaria*, *Cylindrophis* and *Tropidophis* are described. Some of these genera show a considerable departure from the basic myological pattern described for the Boidae. More important, several of these departures embody certain myological modifications paralleling the condition found in the family Colubridae.

Two major tendencies are indicated in the evolution of more complex from simpler, presumably more primitive, myological types. These are: (1) the tendency for median myological elements to become associated with more lateral ones, and (2) a tendency for anterior elements to become morphologically associated with more posterior ones, thereby lengthening considerably certain functional units through fusion of shorter muscles. A number of boid or boid-like groups have independently evolved colubrid-like myological modifications several times in the past. This phenomenon in its variety of forms is termed "myological colubridization." Details concerning the major trends in the evolution of trunk musculature are discussed, as well as their phylogenetic implications.

As a contribution to a much needed wider survey of snake myology, certain of the more important aspects of the epaxial trunk musculature of *Xenopeltis*, *Eryx*, *Calabaria*, *Cylindrophis* and *Tropidophis* are described. Some of these genera show a considerable departure from the basic myological pattern previously described for the Boidae. More important several of these departures embody certain myological modifications paralleling the condition found in the family Colubridae.

INTRODUCTION

Little has been published on the myology of the trunk region of snakes. Mosauer's work in 1935 remains the classic. His tripartite classification of muscle arrangement (boid, colubrid, and viperid) appears to be basically sound, though over-simplified to be useful in detailed evolutionary studies. Myological intermediacy between the typical colubrid and boid types has already been illustrated in one snake genus (Auffenberg, 1958).

I wish to thank Dr. Ernest E. Williams, Museum of Comparative Zoology, who made available most of the specimens on which this study is based. The descriptions are based on a single adult speci-

men of each of the five genera of boid snakes examined with the exception of *Eryx johni*, where, because of their small size several specimens were examined. The myological description is meant to supplement that given by Mosauer, and follows, for the most part, his outline of presentation to facilitate comparison. Not all of the myological elements of the trunk region are discussed, but only those previously shown to be important from a comparative standpoint.

CYLINDROPHIS MACULATUS

M. Semispinalis and Spinalis (SSP, SP)

Unlike the typical boid pattern of a fused semispinalis and spinalis arising from a tendinous arch stretched between the neural spine and postzygapophysis of a single vertebra, in this genus the complex is separated, at least posteriorly, with each head arising more or less from a weakly defined tendinous arch. The spinalis arises by a raphe from the dorso-posterior surface of the *M. multifidus*. The semispinalis arises slightly anterior to this, partly from the dorsal surface of the arch of the same segment, and partly from another tendinous structure to be described below. A few fibers may join the two muscles along their median extent, so that they are not completely separated. Anteriorly, each muscle is provided with a thin flat tendon, directed anteriorly, medially and dorsally.

The latero-posteriorly directed arm of the tendinous arch is inserted on the latero-dorsal surface of the postzygapophysial process of the same vertebra. A much more weakly developed arm is apparently given off of the stronger arch, to run cranio-laterally, inserting on the postzygapophysial process of the preceding vertebra. Thus, the arch is attached in three areas — a neural spine, a more strongly developed arch attached to one postzygapophysis, and a more weakly developed arch extending to a more anterior postzygapophysis.

The origin of the semispinalis is by a raphe on a tendon originating on the dorso-lateral surface of a succeeding neural arch. This tendon then extends cranially to insert on the upper surface of the postzygapophysis of the vertebrae preceding the one forming the origin and insertion of the tendinous arch; thus, the tendon spans three vertebrae. Near the origin of this tendon a thin small muscle arises ventrally and slightly laterally to insert on the medio-posterior surface of the preceding vertebra. The homology of this muscle is unknown, though it appears as though it might be a separated portion of the interarticularis superior that has migrated dorsally and laterally for a short distance. Part of the origin of the semispinalis is along this tendon, where fibers run cranio-dorsally to join the main group arising on the ventral portion of the main tendinous arch. Along its length the semispinalis is also joined by fibers originating along a portion of the multifidus.

The spinalis and semispinalis both span three vertebrae, inserting by means of a long thin tendon into the caudo-dorsal edge of the neural spine of a preceding vertebra.

M. Longissimus Dorsi (ML)

This muscle is similar to that in *Constrictor* and *Sanzina*, with the origin at the cranio-lateral portion of a prezygapophysis. At about the level of the fourth vertebra cranial to its origin the muscle is replaced by a flat tendon, which divides into two parts. The medial portion inserts on the postero-dorsal portion of the neural arch of the ninth vertebra anterior to the origin of the muscle. The lower division of the tendon extends cranially and ventrally to form the medial belly of the retractor costae, inserting on the rib of the ninth vertebra.

The main difference between this series of muscles and tendons in *Sanzina*, *Constrictor* and *Cylindrophis* lie in the lengths of the myological segments. In the latter the longissimus is much shorter than in *Sanzina*, its tendon inserting on the ninth, rather than on the fourteenth rib. In *Constrictor* it inserts on the fifth rib.

M. Multifidus (MM)

In *Cylindrophis* this muscle arises from the dorsal surface of the tendinous arch and is connected to the spinalis by a raphe. It spans two vertebrae to insert on the posterior edge of the neural arch of the third vertebra. A number of fibers originating on the dorso-latero-posterior surface of the neural arch of the vertebra spanned (number 2) join the main group to continue to the common insertion on the third. Some fibers originating in the main belly of the multifidus join with those of the semispinalis.

M. Interarticularis Superior (IAS)

This muscle arises on the dorsal surface of the postzygapophysis of one vertebra, and inserts on the posterior edge of the postzygapophysis of the preceding vertebra. The arrangement is thus similar to that in *Sanzina*, but lacks the small tendinous slip which connects to the next vertebra anteriorly. The thin tendon described above under the spinalis complex, with the small muscle slip, may represent a portion of the interarticularis superior that has migrated dorsally to become associated with the semispinalis and tendinous arch.

M. Costovertebrocostalis (CV)

Unlike the condition in *Constrictor* and *Sanzina*, this muscle seems to arise in only one head; from the ventro-lateral surface of the centrum, extending caudally and laterally to insert on the costal tubercle and neck of the succeeding rib.

The remaining trunk muscles of *Cylindrophis* seem identical to those in *Constrictor*.

TROPIDOPHIS MACULATUS

M. Spinalis and Semispinalis (SP, SSP)

The spinalis of *Tropidophis* arises from the medial portion of a fairly well developed tendinous arch, running cranio-medially to the

posterior portion of a neural spine. The muscle spans nine vertebrae, and is much better developed than the semispinalis, which apparently arises by means of a tendon (shared with the interarticularis superior), and extends cranio-medially to insert on the posterior edge of a neural spine. This insertion is shared with the spinalis portion, and the two muscles become rather well interlaced over their anterior thirds. Thus, only the spinalis arises on the tendinous arch; the semispinalis having abandoned this structure by migrating laterally and then anteriorly along the interarticularis superior. The association of the interarticularis superior with the semispinalis is much more complex in *Tropidophis* than in *Sanzina*.

M. Multifidus (MM)

The multifidus spans four vertebrae, arising along almost the entire length of the tendinous arch. The muscle inserts on the caudal border of the neural arch of a more anterior element. A few fibers are interlaced with those of the interarticularis superior.

M. Longissimus Dorsi (ML)

The longissimus of *Tropidophis* is similar to that found in *Sanzina*, originating on a prezygapophysial process and extending medio-anteriorly to insert on the thirteenth vertebra from the point of origin. At the level of the tenth vertebral element, the muscle is replaced by a flat tendon which divides cranially. The medial, or dorsal portion, inserts on a neural spine, while the ventral portion runs antero-ventrally to form the partial origin of the retractor costae. Near this point a small tendon runs to the thirteenth rib anterior to that at which the longissimus originated.

M. Interarticularis Superior (IAS)

In *Tropidophis* this muscle is bified posteriorly, but fused anteriorly, with a common insertion on a postzygapophysial process. The more medial belly of the muscle spans three vertebrae. For almost the length of one vertebra this unit is represented by a very small tendon. Near the beginning of the muscle fibers themselves (which continue anteriorly) a raphe forms the origin of the weakly developed semispinalis. The latter muscle continues dorso-cranially to form a common insertion with the spinalis. Slightly more anteriorly along the same belly of the interarticularis superior a few fibers become interlaced with those of the multifidus. At the next vertebra anterior to the origin of this belly, the lateral, and thicker belly of the interarticularis superior originates on a prezygapophysial process. Fibers from this muscle fuse with those of the medial belly to form a common insertion on the next vertebra anteriorly. Thus, the interarticularis superior of *Tropidophis* can be considered as a simple digastricus, a unit assumed to be characteristic of the Colubridae by Mosauer, though its homology with the interarticularis superior has already been indicated in *Sanzina* (Auffenberg, 1958).

ERYX JOHNI

M. Semispinalis and Spinalis (SSP, SP)

As is *Cylindrophis maculatus*, this complex is not fused, at least posteriorly, in *Eryx johni*. Furthermore, only the semispinalis originates on a tendinous arch. In this respect it differs from all other boid-like forms examined so far. From the lateral portion of the tendinous arch the semispinalis extends cranially and medially to fuse with the spinalis after passing over one vertebral segment. The spinalis arises by means of a short heavy tendon attached to the antero-lateral portion of a neural spine. It then continues anteriorly to fuse with the semispinalis. Both semispinalis and spinalis insert on the postero-lateral portion of a neural spine. From point of origin to insertion is about seven to nine vertebral segments, with most of the myological elements in the middle of the body spanning nine. The tendinous arch is complete, as in *Constrictor*, *Sanzina*, etc., and also serves as the origin for the multifidus. Certain strands of the interarticularis superior, particularly near the origin of this muscle, are intimately interlaced with those of the semispinalis. In this regard *Eryx* is similar to *Sanzina*, where a similar association is known to occur.

M. Longissimus Dorsi (ML)

This muscle is apparently identical to that found in *Sanzina*, with the segments of the middle of the body spanning nine vertebrae.

M. Multifidus (MM)

The multifidus arises from below the origin of the semispinalis on the same tendinous arch. From the arch the flat, well developed muscle runs cranially to insert on the posterior border of a neural arch at a distance of four vertebrae anterior to the vertebra of origin. A number of fibers originating on the dorso-latero-posterior surface of the neural arch of the vertebrae spanned (numbers two to four) join the main group to continue to the common insertion on the fifth segment. These fibers may actually arise from the belly of the intervertebralis.

M. Interarticularis Superior (IAS)

This muscle arises on the postzygapophysis of one vertebra and inserts on the posterior edge of the postzygapophysis of the preceding vertebra, as it does in most boids, and boid-like forms. However, as indicated above, fibers near the point of origin are connected with those of the spinalis complex, as in *Sanzina*. In addition the interarticularis superior seems to possess a second belly lateral to the one involved with the semispinalis. However, the specimens available for study were quite small, and the exact nature of this association needs clarification.

CALABARIA REINHARDTI

M. Semispinalis and Spinalis (SSP, SP)

This complex is fused in *Calabaria*, arising from a strong tendinous arch on one vertebra and inserting into the postero-lateral portion of the neural spine of a vertebra nine segments cranially. As in *Sanzina* and *Eryx*, the interarticularis superior sends some fibers into the lateral portion of the semispinalis. Mosauer, who apparently examined a specimen of *Calabaria*, did not mention this association. However, unless specifically searched for this connection is difficult to see.

M. Longissimus Dorsi (ML)

This muscle in *Calabaria* is seemingly identical to that in *Sanzina*, and covers nine segments.

M. Multifidus (MM)

The origin of this muscle does not seem to be on a tendinous arch, but on the cranio-lateral portion of the neural spine of one vertebra, extending cranially and laterally to span another vertebra, to insert in a normal fashion on the third. This is the only boid or boid-like form examined in which the multifidus originates in this fashion. The muscle has evidently migrated medially off of the tendinous arch, and onto the neural spine.

M. Interarticularis Superior (IAS)

The origin and insertion of the interarticularis in this genus seems to be normal. A number of fibers form a simple association with the semispinalis. The muscle is only one segment in length.

XENOPELTIS UNICOLOR

M. Semispinalis and Spinalis (SSP, SP)

In *Xenopeltis* this complex is unlike any that I have seen in any other snake. The semispinalis and spinalis portions are essentially fused. Each fused, major unit arises from a fairly well developed tendinous arch stretched between the lateral portion of the neural arch and the neural spine, in a rather normal manner for boid, or boid-like forms. However, additional muscle slips are contributed to the main belly from tendinous arches on preceding and succeeding vertebrae. At least two vertebrae anteriorly contribute such additional fibers, and one posteriorly. The main body of the fused complex covers thirteen to fourteen vertebrae. Each tendinous arch also serves as a point of origin for the multifidus. From the neural spine a very weakly developed tendinous arch stretches to the postero-dorsal portion of the postzygapophysial process of the preceding vertebra. This arrangement is very similar to the one described

above for *Cylindrophis*. This weaker arch is below the main body of the muscle and apparently contributes a few fibers upwards into the main semispinalis-spinalis complex.

M. Longissimus Dorsi (ML)

The longissimus in *Xenopeltis* arises from a well developed tendon attached to the ventro-anterior surface of the prezygapophysial buttress. From this point the long flat muscle extends cranio-medially to divide at about the level of the fourth vertebra. The medial, or dorsal portion continues cranially and medially to insert in a normal fashion on the postero-lateral portion of the neural spine of the ninth vertebra cranial to the point of origin. The lateral belly is continued as a tendon antero-ventrally to eventually become the origin of the medial belly of the retractor costae. At the point of origin of the longissimus a well developed tendon runs ventro-cranially to insert on the rib of the next vertebra anteriorly. A similar attachment is found in *Sanzina*, though it occurs much more anteriorly to the origin of the longissimus.

M. Multifidus (MM)

The multifidus in *Xenopeltis* seems to be normal, arising from a tendinous arch and extending anteriorly to insert into the caudal border of the neural arch of a vertebra three segments anteriorly.

M. Interarticularis Superior (IAS)

This muscle is small, simple, and normal for the boid condition, extending from one postzygapophysial process to the same process on the next vertebra anteriorly.

The transversus dorsalis, costovertebrocostalis, retractor costae, costalis internis superior and interarticularis inferior all seem normal.

The most significant columnar variation beyond that described for *Sanzina* (Auffenberg, 1958) is that the complexity of the semispinalis and spinalis in the anterior and middle of the body is not found posteriorly. In this region each tendinous arch seems to give rise to a separate fused unit of semispinalis and spinalis, and adjacent arches do not contribute fibers to the main belly.

DISCUSSION

The exact phyletic positions of most of the snakes discussed are not clear and the present myological study sheds little light on this problem. Deviations in muscular arrangement are in some cases suggestive of intermediacy between typical boines (such as *Constrictor*) and the Colubridae (as represented by *Coluber*). However, this intermediacy is not interpreted as having important phyletic significance; but rather, seems indicative of some degree of parallel, or convergent, evolution. Thus, it is suggested that a number of boid or boid-like groups have independently evolved colubrid-like myological modifications several times in the past. This phenomenon in its variety of

forms is here termed "myological colubridization." A similar situation regarding certain osteological characters of boid, and boid-like forms, has been intimated by Dowling (1959).

There are two major tendencies indicated in the evolution of more complex from simpler, presumably more primitive, myological types. These are: (1) the tendency for median myological elements to become associated with more lateral ones, and (2) a tendency for anterior elements to become morphologically associated with more posterior ones, thereby lengthening considerably certain functional units through fusion of shorter muscles (Fig. 1.).

In a more detailed fashion, the major trends in the evolution of trunk musculature are here believed to include the following:

1. Abandonment of the tendinous arch as a point of origin by the semispinalis and/or the spinalis and the multifidus.
2. Association of the interarticularis superior with other myological elements through the interlacing of fibers, or by tendinous asso-

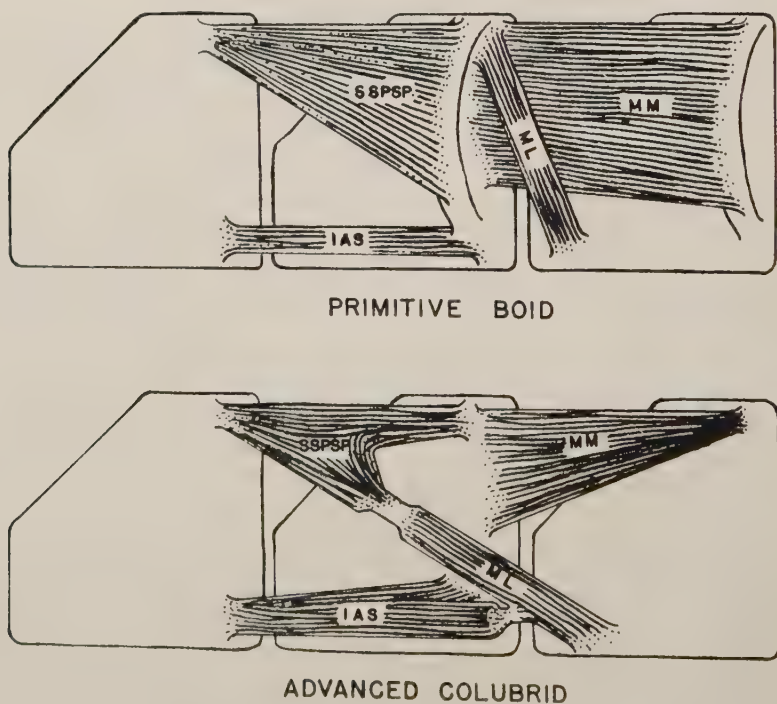


Fig. 1.—Diagrammatic lateral view of primitive and advanced myological types, showing the loss of tendinous arches, migration of the longissimus, and splitting of the spinalis and superior interarticularis complexes in the more advanced condition.

ciations. Primitively this association is with the spinalis complex, or with the multifidus. In advanced forms it is with the longissimus.

3. Splitting of the interarticularis superior posteriorly (forming the digastricus in its variety of forms in some boids, boid-like groups, and other families of snakes).

4. Splitting of the spinalis complex into two muscles, the semispinalis and spinalis. This fission apparently takes place posteriorly in its initial phases, and becomes complete with the cranial migration of the cleft.

5. Association of the semispinalis with other myological units through the interlacing of fibers or by tendinous associations. Primitively this association is with the interarticularis superior. In more advanced forms it is with the multifidus or especially the longissimus.

6. Association of the longissimus with other muscles through the interlacing of fibers or by tendinous associations, such as with the semispinalis, or the interarticularis superior.

7. Loss of osseous insertion of the longissimus.

8. Lengthening of muscle segments through loss of osseous attachments and an increase of interlacing fibers between identical metameric myological segments.

One or more of these trends are seen in many of the boid and boid-like forms. Of the genera examined, the most common modification is one in which the interarticularis superior is associated with a more dorso-medial muscle. This association is usually with the semispinalis, or the semispinalis portion of the spinalis complex if the latter is fused (*Sanzina*, *Eryx*, *Calabaria*, and in a somewhat modified form in *Anilius*). With the exception of *Anilius*, the advanced colubrid condition (association with the longissimus dorsi) has not been recognized in any boid, or boid-like family. In *Anilius* the association is in the form of a common osseous areal origin for both muscles, while in the Colubridae the origin of the interarticularis superior is on the longissimus itself. *Tropidophis* exhibits a singular case in which the association of the interarticularis superior is with the multifidus.

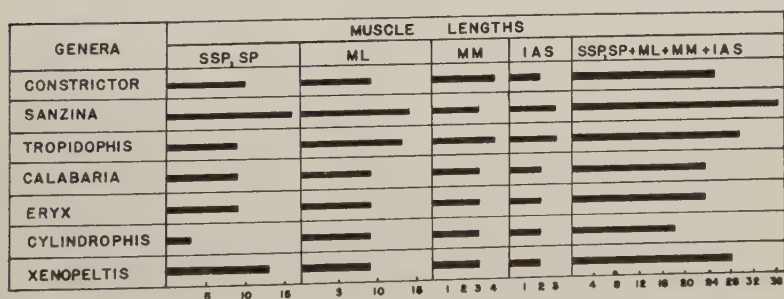


Fig. 2.—Comparative thoracic muscle lengths in various boid, and boid-like snakes

The next most common trends are the division of the spinalis and semispinalis, and the lengthening of particular muscles to cover a greater number of vertebrae. Division of the spinalis complex provides for individual action of two myological units rather than one, in which one of the units is more lateral in action than the other. In the more primitive condition the origin of the spinalis and semispinalis remains on the tendinous arch (*Cylindrophis*). In more advanced types either the origin of the spinalis or semispinalis portions is off of the arch (*Anilius*, *Tropidophis* and *Eryx*). Only in the Colubridae do both muscles lack the arch as a point of origin.

Comparative lengths of the muscle units in genera examined is shown in Figure 2. From these illustrations it is seen that the longissimus, interarticularis superior, and multifidus seem most stable. The spinalis complex is most variable.

The genera also differ in the degree of elongation of any particular muscle. Thus, *Sanzina* possesses the longest spinalis and longissimus muscles; *Constrictor* and *Tropidophis* the longest multifidus, and *Tropidophis* the longest interarticularis superior. Within a single genus comparisons of another type are possible. Thus, *Xenopeltis* possesses a long spinalis complex, but is normal in other units considered; *Cylindrophis* possesses the shortest spinalis complex, but is normal in other units considered; *Eryx* is conservative in all of the units studied, etc.

A comparison of the total length of all myological elements considered important in this study (SSP, SP + ML + MM + IAS) (Fig. 2) shows that of the boid and boid-like genera examined, *Sanzina* has the greatest accumulative length, then *Tropidophis*, *Xenopeltis* and *Constrictor* in respective decreasing lengths. The totals for *Calabaria* and *Eryx* are rather small. *Cylindrophis* has the shortest accumulative length of all.

The next trends in decreasing order of abundance are the associative nature of the spinalis with some other myological element, and the abandonment of the tendinous arch as a point of origin for the multifidus.

Association of the spinalis complex with the interarticularis superior by means of interlacing fibers has been discussed above. In *Anilius* the spinalis is associated with the interarticularis superior by a common areal origin, and with the longissimus by a connecting tendon. In *Xenopeltis* each segment of the spinalis complex is associated with two preceding and one succeeding unit through the interlacing of spinalis fibers originating from the tendinous arches of these vertebrae. In *Coluber* the spinalis arises at the point of origin of the longissimus, a condition approached only by *Anilius* among the boid and boid-like forms examined so far.

The loss of the tendinous arch as an attachment for the multifidus is found in *Anilius* and *Calabaria*. In *Anilius* the fibers originate on the dorsal surface of the neural arch, as they do in the Colubridae. In *Calabaria* the origin of the muscle is unique in that it is not on the arch, but on the cranio-lateral portion of a neural spine.

Two other trends of equal occurrence are the posterior division of the interarticularis superior to form the digastricus, and the abandonment of the tendinous arch as a point of origin for only one of the two members of the spinalis complex.

Among boid and boid-like forms a posterior division of the interarticularis superior is found in *Anilius*, *Eryx* and *Tropidophis*. Mosauer (1938) considered such a condition a colubrid character. The interlacing of the fibers of the interarticularis superior and the spinalis complex (*Sanzina* and *Calabaria*) is here interpreted as a condition leading to the formation of a digastricus, since if these connecting fibers became more numerous and longer a 'Y' or 'V'-shaped muscle would be produced. The condition found in *Cylindrophis*, where a long, thin tendon associated with the semispinalis sends a small slip into the interarticularis superior is apparently unique. In this case the tendon may represent a part of the interarticularis superior that had migrated dorsally and become almost completely separated from the functionally important lower and larger unit.

The semispinalis abandons the tendinous arch in *Anilius*, where the muscle has apparently moved laterally. In *Eryx* the spinalis has moved medially to originate completely on the neural spine. The myological arrangement in the latter is thus similar to that in the Colubridae where the spinalis extends from neural spine to neural spine. However, as far as is known all colubrid snakes completely lack the tendinous arch.

The most uncommon of the trends in myological colubridization among the forms examined is an association of the longissimus with some other unit. In the Colubridae this association is (at the origin of the longissimus) with the spinalis, and (near its insertion) with the interarticularis superior. This condition is apparently approached (in a modified fashion) in the genus *Anilius*, where the muscle is associated with both the semispinalis and the interarticularis superior. However, in this genus the insertion of the longissimus is still on a prezygapophysis, whereas in the Colubridae the insertion is not on a bony element at all, but is continuous with the spinalis. The loss of an osseous insertion for the longissimus and the complete abandonment (and absence) of a tendinous arch by the spinalis and semispinalis are characters not known to occur in the Boidae, or in any closely related groups. Both features apparently represent a culmination in myological modifications, some of which are found in lower phyletic units.

Figure 3 is a diagrammatic illustration of the nature of each of the major myological units discussed so far. Of particular importance are the cases of modifications paralleling those found in the Colubridae. Some of these are: the association between medial and latero-posterior muscles, lengthening of individual myological units, and migration and loss of various types. The probably independent formation of a partially divided interarticularis superior in *Anilius*, *Tropidophis* and *Eryx* (and in a less advanced condition, the simple association of the interarticularis superior and the spinalis complex

in several genera); lengthening of specific muscle segments; loss of the tendinous arch as an origin for the multifidus and/or the spinalis complex, are all considered to be modifications in response to a general tendency to increase efficiency in movement. They seem to have little, if any, phyletic basis. Several degrees and types of modification may be found within a presumable closely related series of genera. The same is true in an analysis in which myological arrangements

GENUS	SSP, SP	ML	MM	IAS
CONSTRUCTOR				
SANZINA				
CALABARIA				
XENOPELTIS				
CYLINDROPHIS				
ERYX				
TROPIDOPHIS				
ANILIUS				
COLUBER				

● POSTZYGAPOPHYSIS
 ● PREZYGAPOPHYSIS
 ▴ NEURAL SPINE

} TENDINOUS ARCH (STRONG)
 } TENDINOUS ARCH (WEAK)
 } POSTERIOR EDGE NEURAL ARCH

Fig. 3.—Diagrammatic representation of the origins, insertions and myological associations of each of the major epaxial thoracic muscles in the genera studied.

are compared with general shape or modes of existence. However, certain minor modifications are associated with type of activity. Thus, in most fossorial snakes the more dorsal muscle units have as their origin and insertion areas proportionately closer to the longitudinal axis of the centrum than do surface dwelling forms. This is well illustrated in the lower neural spines and neural arches of almost all fossorial snakes. In most of these genera the spinalis complex and multifidus are reduced in dorso-ventral thickness. Both of these units are concerned with moving more anterior parts of the body dorsally and laterally. On the other hand, fossorial snakes seem to have better developed longissimus and interarticularis complexes. These muscles are presumably largely involved with lateral movements. In arboreal forms, or at least forms showing some proficiency in an arboreal habitat, where vertical movements of the body are more commonly necessary for efficient progression, the spinalis complex and multifidus are well developed. The neural spines and arches are relatively higher. The lateral members of the epaxial musculature may, or may not be more well-developed.

Figure 4 illustrates the hypothetical evolutionary steps from the much simpler basic boid type of that found in the colubrids. The major steps seem to be (A) association of the interarticularis superior with the fused spinalis complex; (B) separation of the spinalis complex into semispinalis and spinalis; (E) lengthening and anterior migration of the associative fibers of the articularis superior; (F) posterior migration of the longissimus along the semispinalis; loss of the tendinous arch; and, (G) loss of an osseous origin for the semispinalis. No actual examples of certain arrangements have yet been found (steps B, C and D), though very similar conditions have been observed. It is assumed that these slightly modified versions passed through the more basic hypothetical steps. It is quite possible that myological studies on other boid and boid-like forms will disclose arrangements representing these missing stages.

Forms such as *Eryx*, *Tropidophis*, *Xenopeltis*, *Cylindrophis* and *Anilius* seem to represent independently modified arrangements which evolved from the more basic types. Thus, *Cylindrophis* and *Eryx* are approximately at the same level of myological colubridization, since both possess a rather simple arrangement, but with a split spinalis complex (hypothetical step B). However, each genus has taken this arrangement one step further by losing the tendinous arch as a point of origin for one of the two muscles in the complex. In *Cylindrophis* the semispinalis obtains an osseous origin, while in *Eryx* the spinalis does. *Tropidophis* and *Anilius* are also basically at the same level in that they both possess separate semispinalis and spinalis units; possess a tendinous arch; only the spinalis has its origin completely on the arch, and both have a well developed bipartate interarticularis superior, with the origin for the medial belly being well forward (hypothetical step E). However, they are also quite different. In *Tropidophis* the *multifidus* is associated with the interarticularis superior, which in turn spans two vertebrae, rather than one.

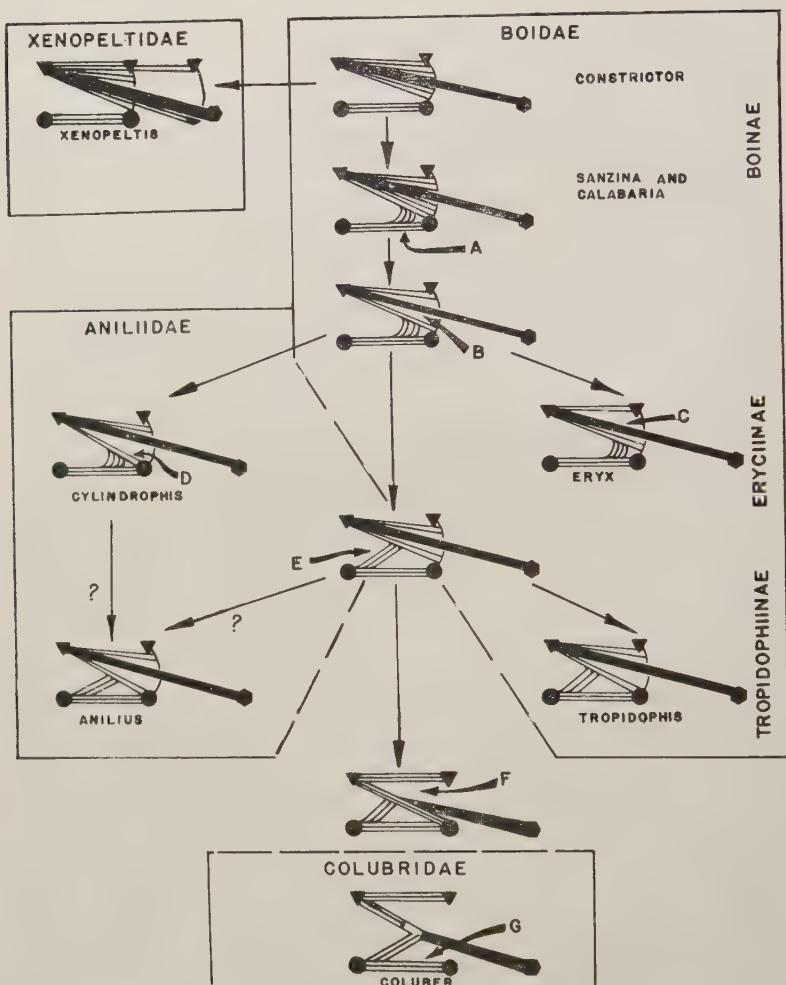


Fig. 4.—Hypothetical evolutionary steps from the simple basic boid type to that found in the colubrids. The major steps are: A, association of the interarticularis superior with the fused spinalis complex; B, separation of the spinalis complex into semispinalis and spinalis; C, lengthening and anterior migration of the associative fibers of the interarticularis superior; D, posterior migration of the longissimus along the semispinalis and loss of a tendinous arch; E, loss of an osseous origin for the semispinalis. Steps F and G are parallel developments in which one member of the spinalis complex has migrated off of the tendinous arch. Steps B, E and F are hypothetical, since no genera have yet been studied which exhibit any of these patterns. *Xenopeltis*, *Cylindrophis*, *Anilius*, *Eryx* and *Tropidophis* all illustrate myological arrangements which, in some form or another, parallel the hypothetical evolutionary steps leading to the colubrid condition. Symbols the same as in Figure 3.

In addition, the arrangement in *Anilius* is much more advanced in degree. The two forms are not necessarily closely related. Both arrangements could have evolved from hypothetical step E, or, more likely, *Tropidophis* from step E and *Anilius* from a *Cylindrophis*-like arrangement (D), in which the origin of the associative fibers of the interarticularis superior had simply migrated anteriorly.

Xenopeltis represents a slightly modified primitive pattern, apparently not on any line leading to higher types. *Sanzina* and *Calabarbaria* are both very close to step A, and perhaps quite close to the line leading to higher types.

When a logical scheme of classification (Dowling, 1959) for these forms is superimposed on this illustration of hypothetical steps in the evolution of trunk musculature, an interesting series of speculative taxonomic considerations becomes evident. Some of these are of interest in regard to possible phyletic arrangements. Thus, *Tropidophis* and *Eryx* can only be considered boids if steps B and E are present in boids. If *Loxocemus* is found to have a pattern identical, or close, to step B this genus should be placed in the Boidae, unless the Eryciinae and/or the Tropidophiinae are to be raised to familial standing. On the other hand, if *Loxocemus* is considered a member of the Aniliidae and the musculature is similar, or identical to that in step E, the Tropidophiinae would have to be raised to familial status. In this event the relationship of *Cylindrophis* and *Anilius* becomes obscure.

Much remains to be learned regarding the relationships of many groups of snakes. Myological studies of broader type may shed considerable light on some of these problems, though it should not be envisioned that such studies will provide all the answers. In some respects such data may raise more questions than they answer. Several additional genera of anilids and the genus *Loxocemus* (regardless of its current or future placement) should be examined in an attempt to clarify questions raised by this study. Also important would be myological study of typhlopids and leptotyphlopids. Of advantage would be a study of the musculature of the more primitive colubrid genera. Some of these may be found to possess a musculature identical to the presently hypothetical step E. More important, such a study would lay the foundation for a more exhaustive examination of more specialized arrangements in the family Colubridae, some of which are suggested in Mosauer's survey and others in observed vertebral peculiarities necessitating modifications of some sort. A pilot study of the trunk musculature of several genera of lizards utilizing different methods of progression above and below the surface of the ground may be quite useful. Parallel myological modifications in limbless lizards and snakes might be sought with profit.

All of these studies, pursued in a systematic and co-ordinated fashion, would contribute greatly to our knowledge of the relationships and functional morphology of the snakes. There is a great need for analysis of all kinds of characters on a generic and super-generic level. Perhaps altogether too much emphasis is currently

being placed on external characters useful in analysis of geographic variation, with the definition of subspecific categories being an end in itself. Such variational studies are useful and important. However, in North America the patterns of geographic variation in snakes are fairly well established, and the information on a large number of species and generic analyses need only be drawn together to provide a more timely and significant statement regarding the nature of the patterns and the reasons for noncoincidence or coincidence.

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The Live Oaks of the Series *Virentes*

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ABSTRACT: Key and descriptions of the 6 species and 1 variety are illustrated, distinctions being based upon morphological, geographic, and ecological (soil tolerance) data. New dispositions include *Quercus minima* Small X *Q. chapmani* Sarg. (= *Q. rolfii* Small), *Q. hemisphaerica* var. *maritima* (= *Q. phellos* β *maritima* Michx. — not *Q. virginiana* var. *maritima* Sarg., a misidentification), *Q. virginiana* Mill. (= *Q. oleoides* var. *quaterna* C. H. Mull.), and *Q. oleoides* var. *sagraeana* (= *Q. sagraeana* Nutt.).

The series *Virentes* of *Quercus* comprises an aberrant natural group within the subgenus *Lepidobalanus*. Typified by *Quercus virginiana*, this small group has come to be known as the "southern live oaks" by reason of its concentration in the southeastern United States and by contrast with the many evergreen species of unrelated series in the southwestern United States, on the coast of California, and in Mexico.

The species of *Virentes* occurring in the United States have, since their original proposals, been given two significantly different treatments. The less conservative treatment of Small (1913, 1933) credits six species to this area, while Sargent (1918) reduces such of these as he treated to the status of varieties under *Quercus virginiana*, simultaneously proposing additional varieties based upon less profound differences. Since neither of these authors concerned himself with the Latin American members of the series, the group has not yet been critically reviewed as a whole. The treatment accorded it by Trelease (1924) incorporated a compromise of Sargent's and Small's views with relatively minor additional modification. In evaluating Trelease's monograph, it must be remembered that he originally set out to do the Latin American species only and that he extended his treatment to the entire North American continent largely by incorporating the treatments of Sargent in the eastern United States and Rydberg in the western United States, subjecting neither to very critical analysis.

The present treatment¹ is motivated by the necessity of a review of the series in preparation for the statement of some evolutionary conclusions to which field and herbarium studies have led me. Although I readily admit the provisional character of some of the conclusions here presented, there are included some geographic, ecological, and morphological evidences of genetic relations (and genetic distinctions) not

¹ I am indebted to the Associates in Tropical Biogeography and the Faculty Committee on Research, both of the University of California, for financial aid in prosecuting the field studies and to the National Science Foundation (project G-2713) for support of both field and herbarium studies upon which this work is based.

heretofore emphasized. An exhaustive field study of the *Virentes* in the southeastern United States, Cuba, and Mexico was initiated, but its continuation would undoubtedly go far toward a satisfactory solution of the problems posed by such plants as the one here called *Quercus virginiana* (juvenile). On the other hand, available ecological descriptions (e.g., Harper, 1913, 1914, 1915, 1927, 1928) have proved, upon checking in the field, to be invaluable in explaining the continued maintenance of *Q. virginiana*, *Q. geminata*, and *Q. minima*. In the course of wide reading in the voluminous ecological literature on the Southeastern Coastal Plain, I was able to find sizable quantities of useful information only in Harper's extensive writings. These works are to be commended to taxonomists and ecologists alike as rich sources of information on the distribution of species and vegetation types in relation to topography and soils, all the more valuable because of their singular freedom from philosophic "isms" and consequent theoretical bias.

Unlike some of the other natural groups in *Quercus*, there is no evidence that the series *Virentes* has been enriched to any great degree by hybridization with the species of other series. Such outcrossing does occur, but it does not result in significant hybrid swarms nor in any important degree of introgression. Hybridization within the series, on the other hand, has had much more tangible results and is to be made the subject of a separate paper in the near future. The natural hybrids involving species of *Virentes* as one or both parents are not here treated exhaustively, although the occurrence of intergrades of hybrid origin is noted where these are of importance to the present study or to the projected evolutionary discussion.

Quercus series *Virentes* Trel., *Mem. Nat. Acad. Sci.* 20:112. 1924.

Dryopsila Raf., *Alsogr. Am.* 25. 1838. (*pro parte*).

Quercus subgen. *Finax* Raf. *Alsogr. Am.* 28. 1838.

Quercus [sect.] *Virginianae* Small, *Man. S.E. Flora* 422. 1933.

Large trees to low rhizomatous shrubs. Bark dark brown or black and deeply furrowed, smooth and hard on vigorous young trunks and branches. Twigs minutely fulvous-stellate-tomentulose (or with glandular puberulence and spreading hairs admixed). Buds rounded, nearly glabrous, usually russet. Leaves evergreen, coriaceous or chartaceous, often quite thick, small or moderate-sized, predominantly elliptic and subentire or obovate and repandly coarse-toothed, margins slightly or very markedly revolute, blades plane or strongly concave beneath, glabrous or nearly so and lustrous above, minutely appressed-stellate-canescens beneath, sometimes with spreading stellate hairs and glandular puberulum in addition; veins highly reticulate, moderately or very prominent beneath or relatively obscure, sometimes impressed above. Staminate catkins stellate-pubescent, the pubescent anthers moderately exerted from the calyces. Fruit annual, moderate-sized, the cups characteristically turbinate, the scales canescens or fulvous.

Range.—Southern Atlantic United States and Cuba to Central West

Texas, Coahuila, and Baja California, and southward along the Gulf of Mexico to Costa Rica.

Type.—*Q. virginiana* Mill.

KEY TO SPECIES AND VARIETIES

1. Leaves with veins markedly impressed above, very prominent beneath, lower surface with prominently spreading hairs.
 2. Leaves markedly concave beneath, plants of the southeastern United States5. *Q. geminata*.
 2. Leaves plane or only slightly concave beneath, plants of Cuba.....
 -6a. *Q. oleoides* var. *sagraeana*.
1. Leaves with veins slightly or not at all impressed above, obscure or only moderately prominent beneath, lower surface with appressed minute stellate tomentulum and at most scattered spreading hairs.
 3. Leaves predominantly broadly rounded apically, the blades broadest above the middle
 4. Low rhizomatous shrubs.
 5. Leaves densely appressed-stellate-tomentulose beneath.
 6. Leaves basally cuneate, usually dimorphic, the upper narrowly oblong and usually entire, the lower broadly obovate and coarsely toothed.....4. *Q. minima*.
 6. Leaves rounded or obtuse at base, various but not dimorphic as above.....1. *Q. virginiana* (juvenile).
 5. Leaves sparingly appressed-stellate beneath or at length glabrate
 -4a. *Q. minima* x *Q. chapmani*.
 4. Trees or at least large shrubs 3 m tall.
 7. Leaves normally three times as long as broad, plants of the southeastern United States.....1. *Q. virginiana*.
 7. Leaves not over twice as long as broad, plants of the Gulf Coastal Plain of Mexico and Central America.....6. *Q. oleoides*.
 3. Leaves predominantly acute, the blades broadest below the middle.
 8. Acorns markedly fusiform, over three times as long as broad, plants of the Cape Region of Baja California.....3. *Q. brandegei*.
 8. Acorns not as much as three times as long as broad.
 9. Acorns barrel-shaped, not twice as long as broad, plants of the Gulf and Atlantic Coast of the United States.
 10. Shrubs.....1. *Q. virginiana* (juvenile).
 10. Trees.....1. *Q. virginiana*.
 9. Acorns subfusiform, often twice as long as broad, plants of the piedmont in the Edwards Plateau of Texas and the Sierra Madre Oriental of Mexico.....2. *Q. fusiformis*.

1. *Quercus virginiana* Mill., *Gard. Dict.*, ed. 8, no. 16. 1768.

Q. sempervirens Walt., *Fl. Carol.* 234. 1788.

Q. virens Sol. in Ait. *Hort. Kew.* 3:356. 1789.

Q. andromeda Riddell, *New Orleans Med. & Surg. Jour.* 9:614. 1853.

Q. virginiana var. *virescens* Sarg., *Bot. Gaz.* 65:446. 1918.

Q. virginiana var. *eximea* Sarg., *Bot. Gaz.* 65:447. 1918.

Q. eximea Trel., *Mem. Nat. Acad. Sci.* 20:116. 1924. (nom. prov.).

Q. andromeda f. *nana* Trel., *Mem. Nat. Acad. Sci.* 20:116. 1924.

Q. oleoides var. *quaterna* C. H. Mull., *Contr. Texas Research Found.* 1:76. 1951. (*pro max. parte, typus excl.*).

Moderate to very large trees with broad spreading crowns and roughly furrowed brown or black bark or maturing as low rhizomatous shrubs less than 1 m tall. Twigs 1.5 to 3 mm thick, densely or sparsely gray- or fulvous-tomentulose with a mixture of appressed stellate and glandular hairs and waxy puberulum, the second season gray and nearly glabrate or usually persistently pubescent. Buds 1.5 to 3 mm long, subglobose or rounded-quadrangular, glossy dark red and glabrous or sparingly puberulent; stipules 2 to 4 mm long, subulate, sparsely pubescent, soon caducous. Leaves evergreen or subevergreen, hard and coriaceous, rather thick or moderately thin, 1 to 15 (usually 3 to 10) cm long, 0.3 to 3 or 4 cm broad, oblong or oblanceolate to obovate, predominantly broadest above the middle, broadly rounded or acute in juvenile forms, cuneate or sometimes rounded basally, entire or coarsely and irregularly few-toothed, especially in juvenile forms, margins nearly plane or minutely revolute, blade flat or (especially in thicker forms) slightly concave beneath, upper surface glossy and glabrous or sparingly stellate-pubescent especially about the base of the midrib, lower surface dull, canescent or green, densely covered with minute appressed-stellate hairs on waxy puberulum, or very sparsely pubescent in the green form, midrib and veins usually glabrous; veins about 7 to 11 on each side and with occasional intermediates, irregularly branching and obviously anastomosing, somewhat prominent above and below or rather obscure. Petioles 1 to 10 mm long, densely or moderately stellate-tomentulose. Staminate catkins 1.5 to 5 cm long, the sparsely tomentulose peduncle rather loosely flowered, the pubescent anthers moderately exserted from the variously pubescent calyx. Pistillate catkins 1 to 4.5 cm long, 2- or 3-flowered distally on the tomentulose peduncle. Fruit solitary or paired on a coarse peduncle 0.5 to 2 or more cm long; cups 8 to 12 mm high, 9 to 15 mm broad, hemispheric to deeply goblet-shaped, usually markedly constricted basally, the scales markedly thickened basally, densely white or silvery tomentulose, the apices dark red and glabrous or puberulent; acorns 15 to 22 mm long, 9 to 15 mm broad, narrowly or broadly barrel-shaped, apex always rounded, glabrous and glossy brown or with a waxy glaucous bloom, about one-third included.

Range. Coastal plain, immediately adjacent to the coast. Virginia to Florida and west to Texas, inland only at the low elevations of peninsular Florida and locally on old beach lines in Louisiana and Georgia.

Quercus virginiana is the largest, most widely spread, and most abundant species of the series and is therefore easily the most prominent. It rarely extends above the coastal prairie and is confined largely to moderately heavy soils, or gravelly soils containing clay, in the immediate vicinity of the coast. It is absent from deep, relatively pure sand over nearly all of its range, its place being taken there by related species. The one exception noted (on the sand dunes of Brooks and Kenedy Counties, Texas) remains unexplained, unless it relates to hybrid influence by *Q. olcoides*. Where the species approaches piedmont topography (e.g., the limestone areas of the Edwards Plateau of

Texas) it is replaced by *Q. fusiformis* with which it intergrades on sites variously intermediate in character between the immediate coast and the inland uplands on which *Q. fusiformis* grows. Outlying limestone outcrops and clay beds on the Coastal Plain in Atascosa, DeWitt, Goliad, and Victoria Counties in Texas harbor true *Q. fusiformis*.

The exact nature of the form referred to *Quercus virginiana* (juvenile) is obscure, for it merges with the species both geographically and ontogenetically while still suggesting some genetic distinctness. The form, like the species, occurs on heavy soil and is confined to the immediate coastal areas. As described in a previous paper (Muller 1951a), *Q. virginiana* develops into a rhizomatous shrub, a form which it maintains indefinitely before assuming tree form. In a pure population of the species the fruiting shrub stage occurs mixed with the mature trees and all gradations between are in evidence. It is my opinion that there exists no genetic difference responsible for the two fruiting forms and that this is not deserving of varietal distinction. The shrub form is therefore treated here as a "juvenile" form of *Q. virginiana*.

Some part of the distinction suggested may result from the influence of hybridization of *Quercus virginiana* with *Q. oleoides*. A few characters of *Q. oleoides* are visible in the extreme southwestern coastal population of *Q. fusiformis* in Texas as well as in some adjacent populations of *Q. virginiana* (described as *Q. oleoides* var. *quaterna*). A recent extensive field study in the northernmost coastal populations of *Q. oleoides* in Tamaulipas failed to reveal a close relationship of that species to the proposed Texan variety. Thus, the southwestern extremity of *Q. virginiana* clearly carries a few characters of *Q. oleoides*, but scarcely enough to prejudice its reference to *Q. virginiana*. Its essential identity with the Atlantic coastal tree and shrubby forms requires the entire assemblage to bear the name here applied. This problem is discussed more fully under the next species following.

Specimens examined:

VIRGINIA: Norfolk Co., *M. D. Blanchard* s. n.; *N. L. Britton* s. n. (*pro parte*, cf. also *Q. minima*); *F. V. Coville* 19; *T. H. Kearney Jr.* 1215, 1224, 1450, 1754; Northampton Co., *M. L. Fernald*, *B. Long* and *J. M. Fogg Jr.* 5292; Princess Ann Co., *A. Chase* 2347; *J. R. Churchill* s. n.; *M. G. Henry* 2577; *L. Hubricht* B2364; *E. C. Leonard* and *E. P. Killip* 271, 289a; *C. D. Mell* s. n.; York Co., *J. W. Chickering* s. n.; *H. W. Henshaw* s. n.; Hollick and *N. L. Britton* s. n. (*pro parte*, cf. also *Q. fusiformis*); *C. H. Merriam* s. n.; *T. Morong* s. n.; *C. H. Muller* 10353; *W. M. Rankin* s. n.; *J. Schneck* s. n.; *G. Vasey* s. n.; *L. F. Ward* s. n.

NORTH CAROLINA: Brunswick Co., *W. W. Ashe* s. n.; *V. H. Chase* s. n.; *F. V. Coville* 132; Cartaret Co., *R. K. Godfrey* 6387; Dare Co., *W. W. Ashe* s. n.; *W. R. Maxon* 10611; New Hanover Co., *H. H. Bartlett* 2549; *W. H. Canby* s. n.; *R. K. Godfrey* 4840; *G. McCarthy* s. n.; County undetermined, *M. Curtis* s. n.; *J. A. Harris* 19558.

SOUTH CAROLINA: Beaufort Co., *T. G. Harbison* 3533; *J. A. Harris* 19714; *J. H. Mellichamp* s. n.; *C. H. Muller* 9939; *C. S. Sargent* s. n.; Berkeley Co., *R. K. Godfrey* and *R. M. Tryon Jr.* 1612; Charleston Co., *K.*

W. Hunt 419d, 521f, 547c, 2668, 3356, 3358; *H. N. Moldenke* 5170 (*pro parte*, cf. also *Q. pumila* and *Q. minima*), 5174; *J. Schneck s. n.*; *J. K. Small s. n.*; *J. K. Small* and *L. M. Bragg s. n.*; Chesterfield Co., *A. E. Radford* 9123; Florence Co., *J. L. Seal* 7; Georgetown Co., *R. K. Godfrey* and *R. M. Tryon Jr.* 1092; *C. H. Muller* 3861, 3862, 3864, 3864a, 3864b; Jasper Co., *C. P. Alexander* 286; *C. Mohr s. n.*; *C. S. Sargent s. n.*; Lexington Co., *E. A. McGregor* 202, 238, 239, 636; Orangeburg Co., *W. W. Eggleston* 4947, 4948; County undetermined, *J. A. Harris* 2140; *J. H. Mellichamp s. n.*

GEORGIA: Camden Co., *C. H. Muller* 10463; Chatham Co., *R. M. Harper* 725; Dougherty Co., *C. Orr* 1, 1a, 1b; Glynn Co., *C. H. Muller* 9921; Lee Co., *W. H. Duncan* 3093; *R. M. Harper* 1151; Liberty Co., *T. G. Harbison* 27; Thomas Co., *E. Eggleston s. n.*; *J. K. Small s. n.*; County undetermined, *Brendel s. n.*; *J. B. Jones s. n.*

FLORIDA: Alachua Co., *T. G. Harbison* 5344; *W. A. Murrill* 180, 472; Brevard Co., *Bates s. n.*; *A. B. Burgess* 622; *A. S. Rhoads* 8395; Broward Co., *W. C. Coker s. n.*; Charlotte Co., *Blodgett s. n.*; Clay Co., *T. G. Harbison* 16293 and/or 7048; Collier Co., *J. K. Small* and *J. P. Dewinkeler* 9925; Dade Co., *E. A. Bessey* 17, 85; *N. L. Britton* 99; *N. C. Cowles s. n.*; *H. N. Moldenke* 5465, 5512, 5854; *M. F. Moseley* 377, 378, 379, 380, 381, 382, 383, 386; *C. A. Mosier* 349, 353, *s. n.*; *C. A. Mosier* and *W. E. Stafford* 61, 62, 76, 77; *W. E. Stafford s. n.*; *J. K. Small* 7255, 8073, 8074, *A.*; *J. K. Small* and *J. J. Carter* 1318, 2482; *J. K. Small* and *G. V. Nash* 69, *s. n.*; *J. K. Small*, *J. W. Small* and *J. P. DeWinkeler* 10326, 10326a, *s. n.*; *A. Rehder* 818; *J. P. Young* 230; DeSoto Co., *C. H. Muller* 9833; Dixie Co., *T. G. Harbison* 69; *C. H. Muller* 9824; Duval Co., *D. Demaree* 20750; Flagler Co., *C. H. Muller* 9905; Franklin Co., *A. W. Chapman s. n.*; *C. H. Muller* 9804, 10261; Gadsden Co., *T. G. Harbison* 3671; Gulf Co., *W. L. McAtee* 1770b; *C. H. Muller* 9801; Hernando Co., *R. N. Jones* 140; Highlands Co., *A. H. Howell* 1072; *J. P. McFarlin* 8432, 8432a; Hillsborough Co., *A. P. Garber s. n.*; Jefferson Co., *C. H. Lighthipe s. n.*; Lafayette Co., *T. G. Harbison* 5565; Lake Co., *Bosanquet s. n.*; *G. V. Nash* 1693; Lee Co., *J. P. Standley* 225; *P. C. Standley* 12776, 52574; Leon Co., *J. H. Beal s. n.*; *N. K. Berg s. n.*; *C. H. Muller* 10471; *E. J. Palmer* 35228, 35231; *Reese* 628, 629, 630, 631, 632; *F. Rugel s. n.*; *A. Steward s. n.*; Levy Co., *T. G. Harbison* 3177; *Reese* 750; Manatee Co., *A. P. Garber s. n.*; *J. H. Simpson* 11, 65, *s. n.*; Marion Co., *C. D. Mell s. n.*; *C. H. Muller* 9830; *L. F. Ward* and *R. Ward s. n.*; Martin Co., *C. H. Muller* 9879; Okeechobee Co., *J. K. Small*, *E. G. Britton*, *N. L. Britton* and *J. P. DeWinkeler* 925a; Orange Co., *F. S. Blanton* 6488, 6543; *J. G. Grossenbacher s. n.*; *M. Meislahn* 42; *H. O'Neill s. n.*; Osceola Co., *E. A. Mearns s. n.*; Putnam Co., *G. Smith* 7617, *s. n.*; Santa Rosa Co., *C. H. Muller* 9780; Seminole Co., *T. G. Harbison s. n.*; *A. P. Garber s. n.*; *H. O'Neill s. n.*; *S. Rapp* 3, 9, 9a, 14, *s. n.*; St. Johns Co., *A. Chase* 7016; *J. A. Harris* 21194; *J. K. Small* and *J. J. Carter* 1441; Taylor Co., *C. H. Muller* 9818, 9819, 9820, 9821; Volusia Co., *A. B. Burgess* 610; *C. H. Muller* 9895; Walton Co., *C. H. Muller* 9784, 9786; Wakulla Co., *J. H. Beal s. n.*; *R. K. Godfrey* and *R. Kral* 53921; *C. H. Muller* 9814; *Reese* 627; *F. Rugel s. n.*; County undetermined, *Beyrich s. n.*; *W. H. Canby s. n.*; *A. W. Chapman s. n.*; *Manigault s. n.*; *W. L. McAtee s. n.*; *W. E. Stafford* 1763.

ALABAMA: Baldwin Co., *C. H. Muller* 9779; Mobile Co., *H. H. Bartlett* 3210; *J. M. Bigelow s. n.*; *B. F. Bush* 218; *D. Demaree* 35104; *C. Mohr s. n.*; *J. Schneck s. n.*; *Van Aller* 1.

MISSISSIPPI: Coahoma Co., *J. L. Alcom s. n.*; George Co., *D. Demaree* 34039; *C. H. Muller* 9974; Hancock Co., *C. H. Muller* 9763; Harrison Co., *A. Dachnowski-Stokes s. n.*; *T. G. Harbison* 3657, 3658; *J. F. Joor s. n.*;

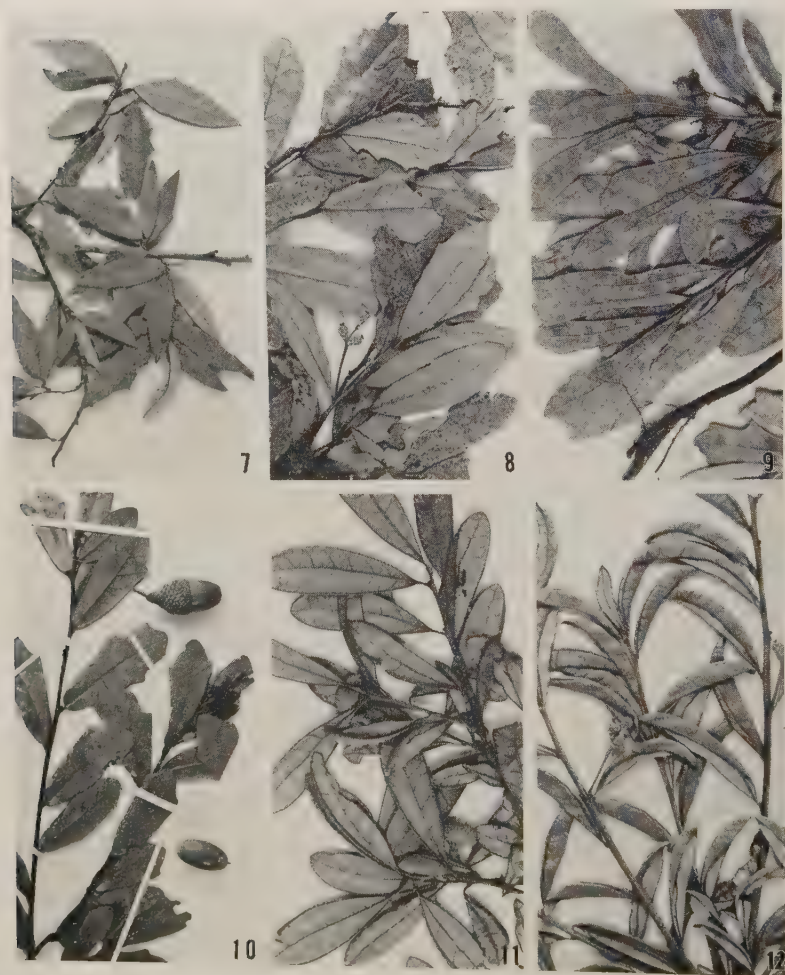
C. H. Muller 10008; *L. H. Pammel s. n.*; *W. D. Sterrett* 3; *S. M. Tracy* and *F. E. Lloyd* 4, 6, 7; *Hinds Co., H. Shearer s. n.*; *Jackson Co., D. Demaree* 33891, 33895, 34520; *E. Hilgard s. n.*; *C. H. Muller* 9766, 9767, 9768, 9769, 9770, 9772, 9958, 9965, 9967, 9969, 9970, 9976, 9977; *C. L. Pollard* 1208;



Figs. 1-6.—*Quercus virginiana*, *Q. fusiformis* and *Q. brandegei*. 1.—*Q. virginiana* Mill. from Baldwin Co., Alabama, *C. H. Muller* 9779. 2. *Q. virginiana* Mill. from Wakulla Co., Florida, *R. K. Godfrey et al.* 53921. 3.—*Q. virginiana* Mill. (juvenile) from Georgetown Co., South Carolina, *C. H. Muller* 3861. 4.—*Q. fusiformis* Small from Brown Co., Texas, *C. H. Muller* 8778. 5.—*Q. fusiformis* Small from Nuevo Leon, Mexico, *J. E. Villareal* 2160. 6.—*Q. brandegei* Goldm. from Baja California (Cape Region), Mexico, *A. Carter et al.* 2173.

J. Skehan 22497; Jefferson Co., *W. B. McDougall* 1178, 1180; Wilkinson Co., *C. H. Muller* 10240.

LOUISIANA: Concordia Parish, *J. Donnell Smith s. n.*; Iberia Parish, *A. P. Beilmann s. n.*; *F. W. Russe Jr.* 6; Natchitoches Parish, *Engelmann s. n.*; *W. D. Sterrett* 36; Orleans Parish, *T. J. Burrill s. n.*; *Riddell s. n.*; St. Mary



Figs. 7-12.—*Quercus brandegei*, *Q. minima* and *Q. geminata*. 7.—*Q. brandegei* Goldm. from Baja California (Cape Region), Mexico, *F. Hester* 6. 8.—*Q. minima* Small from Franklin Co., Florida, *C. H. Muller* 9802. 9.—*Q. minima* Small from Clay Co., Florida, *C. H. Muller* 10327. 10.—*Q. minima* Small X *Q. Chapmani* Sarg. from Broward Co., Florida, *J. K. Small* and *J. J. Carter* 1244 (type of *Q. rolfii* Small). 11.—*Q. geminata* Small from Charleston Co., South Carolina, *K. W. Hunt* 2823. 12.—*Q. geminata* Small from Taylor Co., Florida, *C. H. Muller* 9823.

Parish, *W. D. Sterrett* 9, 11, 13; St. Tammany Parish, *Cocks* 4722; *G. Arsène* 11590, 11742, 12421, 12423, 12428, 12434, 12440, 12441, 12451, 12452, 12454, 12455, 12457, 12460, 12461, 12462, 12466, 12475, 12499, 12500, 12501, 12516; *C. H. Muller* 10256; Tangipahoa Parish, *Cocks* 4716 (type of *Q. virginiana* var. *eximea* Sarg.); Terre Bonne Parish, *C. H. Muller* 9762; Parish undetermined, *Carpenter* s. n.; *C. S. Sargent* s. n.

TEXAS: Aransas Co., *A. Chase* 6046, 4058; *H. von Schrenk* 3; Brazoria



Figs. 13-16.—*Quercus oleoides* and *Q. oleoides* var. *Sagraeana*. 13.—*Q. oleoides* Schl. & Cham. from Veracruz, Mexico, *C. H. Muller* 9477. 14.—*Q. oleoides* Schl. & Cham. from Honduras, *P. Shank* 10782. 15.—*Q. oleoides* var. *sagraeana* (Nutt.) C. H. Mull., from Prov. Pinar del Rio, Cuba, *C. H. Muller* 9851. 16.—*Q. oleoides* var. *sagraeana* (Nutt.) C. H. Mull., from Prov. Pinar del Rio, Cuba, *C. H. Muller* 9877.

Co., *B. F. Bush* 867; *C. H. Muller* 9759, 9760; *F. Lindheimer s. n.*; *E. J. Palmer* 5108; *W. D. Sterrett* 2, 7; *G. B. Sudworth s. n.*; Brooks Co., *C. H. Muller* 8047, 8048, 9683, 9684; Calhoun Co., *C. H. Muller* 3921, 5162, 10028, 10029, 10030, 10031, 10032, 10033, 10034, 10035, 10037, 10038, 10039, 10040, 10041, 10042, 10043, 10044, 10045, 10046, 10047, 10048, 10049, 10050, 10051, 10052, 10053, 10054, 10055a; *B. C. Tharp s. n.*; Chambers Co., *C. H. Muller* 10084; Harris Co., *A. Hayden* 18, 19; Jackson Co., *J. A. Drushel* 10179; *C. H. Muller* 3923, 5099; Jefferson Co., *C. H. Muller* 9761; Kenedy Co., *Bomhard I*; *C. H. Muller* 5016, 5017, 9483; Kleberg Co., *E. R. Bogusch* S-89; Matagordo Co., *F. Lindheimer s. n.*; *E. J. Palmer* 9737; San Patricio Co., *C. H. Muller* 9753, 9754, 9757.

2. *Quercus fusiformis* Small, *Bull. Torr. Bot. Club* 28:357. 1901.
Q. virginiana var. *fusiformis* Sarg., *Bot. Gaz.* 65:448. 1918.
Q. virginiana var. *macrophylla* Sarg., *Bot. Gaz.* 65:447. 1918.

Large rhizomatous shrub or a large tree with rough black bark and spreading crown. Twigs 1.5 to 2.5 mm thick, densely fulvous-tomentulose, glabrescent the second year or persistently pubescent. Buds about 1.5 mm long, subglobose, glossy dark red, puberulent; stipules about 2.5 mm long, subulate, pubescent, usually quickly caducous. Leaves evergreen, hard and coriaceous, 2 to 7 cm long, 0.5 to 2 cm broad, oblong to elliptic or obovate, very polymorphic (one form elongate and acute, another broad and rounded, with all intermediates), apices very acute or rarely broadly rounded, bases cuneate or rounded, entire or irregularly 1- or several-toothed, margins somewhat revolute or nearly flat, upper surface glossy and glabrous or sparsely stellate-puberulent especially near the base of the midrib, lower surface uniformly dense stellate-tomentulose, the hairs appressed upon a variable layer of waxy puberulence; veins 8 to 10 on each side with occasional intermediates, irregularly branched and anastomosing, very inconspicuous above or slightly raised, scarcely prominent beneath; petioles 2 to 8 mm long, densely tomentulose. Staminate catkins 3.5 to 4.5 cm long, rather loosely flowered on a sparsely tomentose and glandular peduncle, the hairy anthers somewhat exserted from the moderately pubescent calyx. Pistillate catkins 1.5 to 5.5 cm long, 2- or 3-flowered distally or many-flowered along their lengths. Fruit solitary, paired, or in threes on a coarse peduncle 1.5 to 8 cm long; cups 7 to 10 mm high, 7 to 12 mm broad, goblet-shaped, somewhat constricted basally, the scales moderately thickened basally, densely white-tomentose, the apices dark red and puberulent; acorns 1.5 to 2 cm long, 1 to 1.3 cm broad, narrowly ovoid to subfusiform, glabrous and dull brown, one-third or one-half included.

Range.—Piedmont and coastal plain, from Oklahoma and the Edwards Plateau region of Texas south along the Sierra Madre Oriental and outlying ranges of Coahuila and Nuevo Leon into southern Tamaulipas.

The form of *Quercus fusiformis* with elongate and acute leaves with plain margins and very elongate fruiting peduncles which is concentrated in northeastern Mexico is reminiscent of *Q. brandegei*. The broad and obtuse leaves and shorter peduncles of the Edwards

Plateau and coastal plain populations of Texas more nearly approach *Q. virginiana* whose influence apparently differentiated this species from *Q. brandegei*. The Texan form of *Q. fusiformis* extends also into Mexico.

In previous treatments (e.g., Sargent, 1918; Trelease, 1924; Muller, 1951b) all of the coastal plain population was regarded as belonging to *Q. virginiana* while only the extremes of the thick-leaved shrubby form of the Edwards Plateau and adjacent Mexico were referred to *Q. fusiformis*. In the present treatment the entire Texan population is included in *Q. fusiformis* except for a small portion in the extreme southeast corner of Texas which gradually diminishes in prominence as it extends westward along the immediate coast. This modification has resulted from the application of a different method which might well be explained here.

Certain similarities of the Mexican portion of *Q. fusiformis* to *Q. brandegei* of Baja California early suggested the hypothesis that *Q. fusiformis* was differentiated from *Q. brandegei* under the influence of introgression by *Q. virginiana*. A biometric analysis of the three populations (in press elsewhere) confirmed this hypothesis. It became obvious that the best method of distinguishing between *Q. virginiana* and *Q. fusiformis* lay in the use of those characters in which *Q. virginiana* and *Q. brandegei* differ. This *a priori* choice of distinguishing characters could be valid, of course, only if the hypothesis of hybrid origin were correct. Their use, therefore, required the previous application of the biometric analysis. The three principal differences are fruit shape, leaf shape, and pubescence of the lower blade surface. In all three of these *Q. fusiformis* is intermediate between *Q. brandegei* and *Q. virginiana*. Since there exists also a high degree of correlation amongst them, it follows that these are better characters for the distinction of *Q. fusiformis* from *Q. virginiana* than the much less fundamental character of habit upon which *Q. fusiformis* was largely based.

The strict application of the criteria thus chosen has resulted in a separation between species that coincides with a geographic and ecological difference of great import. East of the Sabine River, *Q. virginiana* occurs on a variety of soils (except pure sand) along the immediate coast. Its occurrence inland in Louisiana, Florida, and Georgia appears to be dependent upon low elevation coincident with old beach lines. This extreme restriction to maritime situations continues into Texas in those specimens lacking characters of *Q. brandegei*. This latter species is widely distributed on piedmont slopes and along canyon floors in the Cape Region of Baja California. Although individuals of *Q. fusiformis* may closely approach the coast, no typical *Q. virginiana* extends very far inland from the coast. The inland forms carry some of the morphological characters of *Q. brandegei* and apparently also its ecological characters which permit them to grow in piedmont and other inland situations.

In the southwestern extremity of the range of *Q. virginiana*, its

distinction from *Q. fusiformis* is confused by what is apparently introgression of both by *Q. oleoides*. The liveoaks of the triangle bounded by Frio, Kenedy, and Calhoun Counties, Texas, clearly exhibit some characters of *Q. oleoides*. No acceptable solution of this problem is as yet possible. Graphic analysis of a three-fold introgression is notoriously difficult in any situation, but the fact that some of the characters of *Q. oleoides* obscure the best diagnostic characters of *Q. virginiana* makes this problem manifestly impossible.

In the light of this difficulty we are perhaps not justified in drawing any conclusions more definite than these: (1) there exists some correlation between the incidence of characters of *Q. oleoides* and the distribution of live oaks on dune sand areas along the Texas coast and on the coastal plain; (2) the obscurity of the distinction between *Q. virginiana* and *Q. fusiformis* in the same general area is due to the presence of *Q. oleoides* characters in the population; (3) some of the specimens (here cited under *Q. virginiana*) do not rightly pertain to that species *sensu strictu* and cannot be referred elsewhere with confidence.

It should be pointed out that *Q. oleoides* var. *quaterna* was described on the basis of this melange. Unfortunately, the type of this variety belongs to *Q. fusiformis* and the residual group is once more without a name. I propose to leave it unnamed within *Q. virginiana* with emphasis upon the fact that it owes its unique variability to the genetic influences of *Q. oleoides* and *Q. brandegei* (through *Q. fusiformis*).

Specimens examined:

OKLAHOMA: Comanche Co., *T. G. Harbison s. n.*; *C. H. Muller* 10161, 10162, 10163; *G. T. Robbins* 2859; Kiowa Co., *U. T. Waterfall* 11265.

TEXAS: Atascosa Co., *V. L. Cory* 11672; *E. J. Palmer* 10787, 10792, 11234, 12915; Austin Co., *H. Wurzlow s. n.*; Bastrop Co., *E. R. Bogusch* 1086; Bell Co., *S. E. Wolff* 3407; Bexar Co., *L. Berlandier* 984; *B. F. Bush* 1268; *H. Eggert s. n.*; *V. Havard s. n.*; *G. Jermy s. n.*; Blanco Co., *C. H. Muller* 8702; Bosque Co., *L. H. Shinnners* 10419; Brown Co., *C. H. Muller* 8778; *E. J. Palmer* 26779, 29498; *H. L. Shantz s. n.*; Burnet Co., *Gould, Brown and Celerier* 5479; collector undetermined (Biltmore collection) 14888; Callahan Co., *C. H. Muller* 8790; Coke Co., *C. H. Muller* 8671; *E. J. Palmer* 12464; Coleman Co., *C. H. Muller* 8782; Colorado Co., *J. Byars s. n.*; Comal Co., *F. Lindheimer* 332, 520, 1184, 1185, 1186, 1187, 1188; *E. J. Palmer* 12202; Concho Co., *C. H. Muller* 8676; Crockett Co., *C. H. Muller* 5152; Dallas Co., *V. L. Cory* 243; *De Witt Co., V. L. Cory* 26582; *C. H. Muller* 3913; *M. Riedel s. n.*; Dimmit Co., *E. J. Palmer* 33777; Duval Co., *C. H. Muller* 8056; Eastland Co., *C. H. Muller* 8763; Edwards Co., *V. Bailey s. n.*; *F. Shreve* 9926; Erath Co., *L. C. Gough s. n.*; Frio Co., *C. H. Muller* 5019; *W. Trelease s. n.*; Galveston Co., *F. W. Mally s. n.*; Gillespie Co., *G. Jermy* 99, 100; Goliad Co., *M. Bomhard IV*; *H. Eggert s. n.*; *C. H. Muller* 8034; Grayson Co., *E. F. Owens* 509, 702; Hays Co., *E. J. Palmer* 12100, 12130; Hood Co., *H. Eggert s. n.*; *E. J. Palmer* 6508; *L. H. Shinnners* 10348; Karnes Co., *Johnson* 1609; Kendall Co., *E. J. Palmer* 9816; Kerr Co., *V. L. Cory* 52387, 52388; *Lacey s. n.* (type); *E. J. Palmer* 12224; *A. A. Heller* 1616; Kimble Co., *D. Axelrod s. n.*; *C. H. Muller* 3952, 3952A; Kinney Co., *V. L. Cory* and *H. B. Parks* 26630; *E. A. Mearns* 1326, 1369, 1415; *C. H. Muller*

5043; Lampasass Co., *C. H. Muller* 8692; La Salle Co., *E. J. Palmer* 11292; Lavaca Co., *G. L. Fisher s. n.*; Lee Co., *E. Hall* 599; Llano Co., *G. L. Fisher* 37177; *B. C. Tharp s. n.*; Mason Co., *C. H. Muller* 8679; Maverick Co., *C. H. Muller* 4058; *Schott s. n.*; McLennan Co., *C. H. Muller* 3900; Menard Co., *L. C. Hinckley* and *L. Hinckley* 175; *C. H. Muller* 5026; *E. J. Palmer* 11896; Nolan Co., *C. H. Muller* 8670; *E. J. Palmer* 13749; Nueces Co., *A. A. Heller* 1542; Pecos Co., *M. E. Jones* 26069; *C. H. Muller* 5047; San Patricio Co., *A. A. Heller* 1569; San Saba Co., *E. J. Palmer* 11779, 11786, 11787, 11847; Shackelford Co., *C. H. Muller* 8563; Somervell Co., *L. F. Ward s. n.*; Stephens Co., *C. H. Muller* 8759; Sutton Co., *E. O. Wootton s. n.*; Tarrant Co., *G. W. Letterman s. n.*; *J. Reverchon* 910; *A. Ruth* 648; Taylor Co., *W. L. Tolstead* 5796; Terrell Co., *L. C. Hinckley* and *L. Hinckley* 377; *G. L. Webster* 491; Tom Green Co., *C. H. Muller* 8675; *E. J. Palmer* 12402; *M. Souldard s. n.*; *E. O. Wootton s. n.*; Travis Co., *E. Hall* 598; *W. H. Morgan* 3791; *C. H. Muller* 3942; *R. H. Painter* 141, 142, 143; *R. W. Strandtmann s. n.*; *B. C. Tharp* 8434, 44434; *M. S. Young s. n.*; Uvalde Co., *H. C. Cutler* 798; *I. M. Johnston* and *C. H. Muller* 1; *C. H. Muller* 5091, 5091A; *Edw. Palmer* 1279 (*pro parte*, cf. also *Q. virginiana*); *H. von Schrenck s. n.*; *E. Whitehouse* 603; Valverde Co., *H. C. Hanson* 443; *I. M. Johnston* and *C. H. Muller* 5, 6; *E. J. Palmer* 12954; *J. N. Rose* and *W. R. Fitch* 17960; Victoria Co., *J. D. Mitchell s. n.*; *C. H. Muller* 3918, 3919 (type of *Q. oleoides* var. *quaterna*), 3920; Washington Co., *E. Brackett s. n.*; Williamson Co., *C. H. Muller* 8718; *Edw. Palmer* 1280; Wilson Co., *E. J. Palmer* 9199; Young Co., *J. Reverchon s. n.*; County undetermined, *L. Berlandier* 266 and/or 543, 774 and/or 930, 2360, 2414, 2473, 2476; *J. M. Bigelow* 127, *s. n.*; *S. F. Blake* 1379; *B. E. Fernow s. n.*; *V. Havard s. n.*; *F. Lindheimer* 31790; *E. F. Owens* 510; *Edw. Palmer* 1276; *J. Reverchon* 3670; *C. Wright s. n.*

MEXICO: Coahuila, *E. Marsh* 518; *Edw. Palmer* 299, 1274; *F. L. Wynd* and *C. H. Muller* 285; Nuevo Leon, *L. Berlandier* 1335; *W. H. Canby*, *C. S. Sargent* and *W. Trelease* 227; *J. A. Drushel* 9695, 9696; *M. T. Edwards* 294; *Fernand* 2169; *A. Gavia* 2169; *J. Gregg* 222; *Grizzly s. n.*; *L. A. Kenoyer s. n.*; *Manning* and *Manning* 53400a; *M. Martinez* 21; *C. H. Muller* 580, 581, 2013, 2669; *C. G. Pringle* 2099; *C. S. Sargent s. n.*; *R. A. Schneider* 1122; *W. Trelease* 119; *J. E. Villarreal* 2156, 2160; *S. S. White* 1462; Tamaulipas, *H. H. Bartlett* 10001, 10766, 10901; *H. S. Gentry* 6747; *Manning* 53382; *M. Martinez* 53; *C. H. Muller* 9685, 9686, 9687, 9689; *Edw. Palmer* 264; *A. J. Sharp*, *H. A. Crum* and *W. B. Fox* 50323; *H. W. Viereck* 301.

3. *Quercus brandegei* Goldm., *Contr. U. S. Nat. Herb.* 16:321. 1916.

Moderate or large tree to 18 m tall with furrowed gray bark and broad spreading crown. Twigs 1.5 to 2.5 mm in diameter, densely stellate-tomentulose and waxy puberulent, at length glabrate or variously persistently pubescent. Buds about 1.5 mm long, subglobose, glossy dark red, puberulent; stipules about 3 mm long, subulate, pubescent, usually deciduous. Leaves evergreen, hard and coriaceous, 3 to 7 cm long, 1 to 2 or rarely 3 cm broad, elongate-oblong or sometimes narrowly elliptic, acute or rarely obtuse, basally rounded or merely obtuse, entire or irregularly coarsely 1- to several-toothed, the margins flat or very slightly revolute, upper surface glabrous and glossy or sparsely stellate-puberulent especially about the base of the midrib, lower surface uniformly canescent-stellate-tomentulose, the

hairs appressed upon a dense waxy puberulence; veins about 8 or 10 on each side with irregular intermediates, variously branching and anastomosing, inconspicuously raised on both surfaces; petioles 2 to 7 mm long, densely tomentulose. Staminate catkins about 2.5 to 3.5 cm long, moderately loosely flowered on a densely tomentulose peduncle, the pubescent anthers moderately exerted from the pubescent calyx. Pistillate catkins 1 to 3 or more cm long, 1- to 3-flowered at the apex. Fruit solitary or paired on a coarse peduncle to 6 cm long; cups about 12 mm high and 12 mm broad, deeply goblet-shaped, usually markedly constricted basally, the scales basally thickened and densely white-tomentose, the apices dark red and puberulent; acorns 3 to 4.5 cm long, 1 to 1.2 cm broad, fusiform, the apex attenuately beaked, glabrous and dull brown with a glaucous bloom, one-fourth or less included.

Range.—Piedmont of the Sierra de la Laguna, Cape Region of Baja California, Mexico.

Quercus brandegei is unique in the series *Virentes* in the extremely fusiform acorns and its great isolation from the other members of the series. Furthermore, it occupies generally more rocky and well-drained sites than the other members of the group, a character it shares with *Q. fusiformis*, its closest relative.

Specimens examined:

MEXICO: Baja California, *T. S. Brandegei s. n.*; *A. Carter* 2713; *A. Carter, A. M. Alexander* and *L. Kellogg* 2173, 2455; *H. S. Gentry* 4361, 11830; *H. S. Gentry* and *W. B. Fox* 11866; *F. Hester* 2, 3, 4, 5, 6, 7, 8; *M. E. Jones* 24476, 24477; *M. Martinez* 6; *C. H. Muller* 10548, 10549, 10550, 10551, 10597, 10598, 10599; *E. W. Nelson* and *E. A. Goldman* 7422, 7475 (type); *I. L. Wiggins* 5640.

4. *Quercus minima* Small, *Bull. Torr. Bot. Club* 24:438. 1897.

Q. virens var. *dentata* Chapm. *Fl. So. St.* 421. 1860.

Q. virginiana var. *minima* Sarg. *Silva* 8:101. 1895.

Q. succulenta Small, *Fl. S.E.U.S.* 2 ed. 1332. 1913.

Q. virginiana var. *dentata* Sarg., *Bot. Gaz.* 65:448. 1918.

Q. geminata var. *succulenta* Trel., *Mem. Nat. Acad. Sci.* 20:115. 1924.

Shrub 2 to 10 dm tall spreading by rhizomes. Twigs 1.5 to 2 mm thick, from densely silvery or fulvous stellate-tomentulose at length glabrate and dark red. Buds about 1.5 mm long, subglobose, glossy red, sparingly pubescent; stipules about 3 mm long, subulate, sparingly pubescent, quickly caducous. Leaves evergreen, hard and coriaceous, highly (constantly) polymorphic, the individual plants rarely uniform for one leaf type, the lower leaves characteristically large and toothed or lobed, the upper usually narrowly oblong and entire, the narrow upper leaves tending to hold their pubescence more persistently than the broad lower ones, the narrow form 2 to 5.5 cm long, 0.5 to 1.6 cm broad, oblanceolate, entire or few-toothed near the acute or rounded apex, the base narrowly cuneate, the broad form 4.5 to 11.5 cm long, 2 to 5 cm broad, broadly oblanceolate to narrowly obovate, coarsely

and irregularly toothed in the upper half or full length, obtuse or acute, broadly cuneate, margins slightly revolute, upper surface glabrous and glossy or sparingly stellate about the base of the midrib, lower surface densely or sparsely silvery appressed-stellate-puberulent, this persistent or on some of the broad lower leaves variously deciduous, the midrib and principal veins glabrous; veins 4 to 12 on each side, very irregular, the higher numbers in the narrow leaves, much branched and obviously anastomosing, slightly raised above, rather prominent beneath, the reticulum obscure; petioles 1 to 5 mm long, stellate-pubescent. Staminate catkins 4 to 5 cm long, rather loosely flowered, the peduncle fulvous-stellate-tomentulose, the pubescent anthers finally well exerted from the pubescent calyx. Pistillate catkins 3 to 10 cm long, 2-to several-flowered, the peduncle fulvous-pubescent but glabrate with the twigs. Fruit solitary or paired on peduncles 0.5 to 3 cm long; cup 8 to 16 mm high, 10 to 15 mm broad (in one form only 5 mm high and 7 mm broad), deeply goblet-shaped, usually markedly constricted basally, the scales silvery tomentose with puberulent or glabrous red apices protruding, the bases sometimes strongly thickened; acorns 15 to 20 mm long, 8 to 12 mm broad (in one form smaller), glabrous and rather glossy brown, one-fourth to one-third included or more.

Range.—Sandy coastal plain, southeastern North Carolina, Georgia, Florida, and Mississippi.

While no type specimen was designated for *Quercus virens* var. *dentata*, there exists in the herbarium of the New York Botanic Garden a mixture of material collected by Chapman about Apalachicola some of which represents the present concept of *Q. minima*. The species is typified by Sargent's plate 396 (Silva 8:101. 1895), while the element of this mixture illustrated by Trelease (Mem. Nat. Acad. Sci. 20: pl. 201A. 1924) is a hybrid of *Q. minima* and *Q. geminata*. These two species frequently occur together, the latter usually on the deeper sand substrata, and sporadic hybrids between them are occasionally encountered. The aberrant form designated as *Q. succulenta* Small (and *Q. geminata* var. *succulenta* Trel.) owes its resemblance to *Q. geminata* to this origin.

Although *Quercus minima* overlaps the range of *Q. virginiana*, its restriction to sand substrata apparently so isolates it from the clay-inhabiting tree species that no great hybridization occurs and the two remain distinct. The free fruiting of *Q. minima* in the form of a low rhizomatous shrub readily distinguishes it from the rhizomatous juvenile form of *Q. virginiana* (in which the twig pubescence and leaf characters are also distinctive).

Specimens examined:

NORTH CAROLINA: Brunswick Co., *W. W. Ashe* s. n.

SOUTH CAROLINA: Beaufort Co., *A. Cuthbert* 718; *J. H. Mellichamp* s. n.

GEORGIA: Camden Co., *F. S. Blanton* 6450; Charlton Co., *W. W. Ashe* s. n.; *W. H. Duncan* 7434; McIntosh Co., *C. H. Muller* 9926, 9927, 9930; Mitchell Co., *R. M. Harper* 1167; County undetermined, *R. M. Harper* 1577.

FLORIDA: Alachua Co., *W. W. Ashe* s. n.; *T. G. Harbison* 5306; Baker

Co., *W. W. Ashe s. n.*; Bay Co., *W. W. Ashe s. n.*; *H. J. Banker* 3495; Brevard Co., *A. Fredholm* 5739, 5768, 5779, 6064; *G. G. Hedgcock s. n.*; Calhoun Co., *C. H. Muller* 10480, 10481; Clay Co., *C. H. Muller* 10326, 10327; Dade Co., *H. C. Cowles s. n.*; *H. N. Moldenke* 717, 777, 3666, 5461, 5667; *C. A. Mosier s. n.*; *F. Rugel s. n.*; *W. E. Safford s. n.*; *C. L. Simpson s. n.*; *J. K. Small* 7266, *s. n.*; *J. K. Small* and *J. J. Carter* 550, 2481; *G. B. Sudworth s. n.*; Dixie Co., *C. H. Muller* 10287; Duval Co., *A. H. Curtiss* 2591, 2597 and/or 4597 (*pro parte*, cf. also *Q. geminata*), 4190, 6432, 6432a, *s. n.*; *H. D. Keeler s. n.* (*pro parte*, cf. also *Q. virginiana*); Flagler Co., *C. H. Muller* 9900, 9901, 9913; Franklin Co., *A. W. Chapman s. n.* (type of *Q. virens* var. *dentata*); *C. H. Muller* 9802, 10258, 10259, 10269; *C. Mohr s. n.*; Highlands Co., *T. G. Harbison* 4617; *J. K. Small*, *J. P. DeWinkeler* and *C. A. Mosier* 11361; Lafayette Co., *T. G. Harbison* 5574; Lake Co., *G. V. Nash* 520, 1762; Lee Co., *J. N. Harshberger s. n.*; *A. S. Hitchcock* 338; *H. N. Moldenke* 1012; *J. P. Standley* 165, 289; Manatee Co., *C. H. Muller* 10295, 10296; Reasoner Bros. 405; *J. H. Simpson* 22; Okeechobee Co., *A. H. Howell* 1042; Osceola Co., *A. H. Howell* 993; *E. A. Mearns s. n.*; Putnam Co., *C. H. Muller* 10307, 10308, 10309, 10314, 10315; Seminole Co., *S. Rapp* 21; St. Johns Co., *J. A. Harris* 19896; Wakulla Co., *W. W. Ashe s. n.*; *C. H. Muller* 9816; Walton Co., *C. H. Muller* 9790, 9797; County undetermined, *A. W. Chapman s. n.*; *A. H. Curtiss s. n.*; *H. C. Cowles* 236, 237; *Hubbard s. n.*; *Leavenworth s. n.*; *J. K. Small s. n.*

MISSISSIPPI: Jackson Co., *C. H. Muller* 9963, 9964.

4a. *Quercus minima* Small $\times$ *Q. chapmani* Sarg.

Q. rolfsii Small, *Fl. S.E.U.S.*, 2 ed. 1332. 1913.

Q. geminata var. *succulenta* f. *rolfsii* Trel., *Mem. Nat. Acad. Sci.* 20:115. 1924.

Low rhizomatous shrub. Twigs 1 to 2 mm thick, from densely fulvous-glandular or gray tomentulose soon glabrate and dark reddish brown. Buds about 1.5 or 2 mm long, subglobose, glabrous and glossy red. Stipules about 3 mm long, subulate, pubescent, soon caducous. Leaves evergreen, thin and coriaceous, 2.5 to 5 cm long, 1 to 2.5 cm broad, elliptic to oblong or narrowly obovate, broadly rounded apically and basally, coarsely or obscurely round-toothed or shallowly lobed about the apex or rarely entire, margins somewhat revolute, upper surface glossy and glabrous, lower surface dull, minutely and sparsely puberulent with appressed stellate and simple hairs; veins about 6 or 7 on each side with occasional intermediates, irregularly branching and obviously anastomosing, raised above and quite prominent beneath; petioles 1.5 to 2 mm long. Staminate catkins 3 to 4 cm long, rather loosely flowered on a densely stellate-pubescent peduncle, the pubescent anthers somewhat exerted from the slightly pubescent calyx. Pistillate catkins not seen. Fruit solitary or paired on a coarse peduncle 1 or 2 cm long; cup 12 to 15 mm high, about 14 mm broad, deeply goblet-shaped, strongly constricted basally, the scales basally thickened, silvery tomentose, the puberulent apices dark red; acorn 2 to 2.5 cm long, 0.9 to 1.2 cm broad, oblong, glabrous and glossy brown, about one-third to one-half included.

Range.—Coastal plain, local the full length of eastern Florida.

The tomentulose young twigs, pubescent anthers, and the fruit of this form are all typical of *Quercus minima* and its close relatives in the series *Virentes*, while the prompt glabrescence of the twigs, the leaf outline, and the sparse puberulence of the lower leaf surface are typical of *Q. chapmani*. These two species occur intermixed over many hundreds of square miles. The herbarium specimens identified as *Q. rolfsii* are few in number, but they represent widely separated portions of peninsular Florida. They exhibit some characters, notably size and shape of the fruit, which are not to be found in either *Q. minima* or *Q. chapmani*. The dismissal of *Q. rolfsii* as a hybrid of these two species was therefore impossible on the basis of existing herbarium material. A field study of the problem yielded populations of hybrids locally within the widespread association of the parents. In these typically back-crossing and segregating hybrid populations one invariably found some individuals with the characters of *Q. rolfsii* (e.g., C. H. Muller 10323, 10324, 10325). Those characteristics unique to this form apparently emerge from the complementary effect of *Q. minima* and *Q. chapmani* and are to be found only in the F₁ progeny (or similar intermediates) and not in those hybrids perceptibly diluted by either back-crossing or segregation.

The forms represented by *Quercus virginiana* var. *pygmaea* Sarg. (Bot. Gaz. 65:449. 1918.—*Q. minima* f. *pygmaea* Trel., Mem. Nat. Acad. Sci. 20:115. pl. 201B. 1924) and by *Q. minima* f. *reasoneri* Trel. (l.c., pl. 200B, but "*Quercus geminata reasoneri*" on the plate) belong with *Q. chapmani*. If these are at all related genetically to the species of *Virentes*, it is through dilute hybridization.

Quercus chapmani Sarg., which Small regarded as a species of the series *Virentes*, appears rather to belong with *Q. sinuata* Walt. in the series *Durandiaeae* Trel. in which its appressed stellate pubescence of the lower leaf surface is typical, being extremely minute, silvery, and unmixed with trichomes of any other sort.

Specimens examined:

FLORIDA: Broward Co., J. K. Small and J. J. Carter 1244 (type of *Q. rolfsii* Small); J. K. Small and P. Wilson s. n.; Clay Co., C. H. Muller 10323, 10324, 10325; Orange Co., Baker s. n.

5. *Quercus geminata* Small, Bull. Torr. Bot. Club 24:438. 1897.
Q. virens var. *maritima* Chapm., Fl. So. St. 421. 1860.—not *Q. maritima* Willd., Sp. Pl. 4 ed. 4:424. 1805.
Q. virginiana var. *maritima* Sarg., Silva 8:100. 1895.
Q. virginiana var. *geminata* Sarg., Bot. Gaz. 65:445. 1918.
Q. virginiana var. *geminata* f. *grandifolia* Sarg., Bot. Gaz. 65:446. 1918.
Q. geminata f. *maritima* Trel., Mem. Nat. Acad. Sci. 20:115. 1924.
Q. geminata var. *grandifolia* Trel., Mem. Nat. Acad. Sci. 20:115. 1924.

Small or moderate trees 2 to 12 m tall (or sometimes reaching 20 m) with rough hard furrowed bark. Twigs 2 to 3 mm thick, from fulvous and glandular velvety-stellate-tomentulose gradually glabrate, the lenticels scarcely prominent. Buds to 2.5 mm long, subglobose, red-

dish brown and sparingly puberulent; the stipules 3 to 4 mm long, concave-spatulate, sparsely pubescent, soon deciduous. Leaves evergreen or subevergreen, 3 to 6 or even 12 cm long, 1 to 3 or 4.5 cm broad, oblanceolate to obovate, acute or broadly rounded, basally tapered or rarely rounded, strictly entire, the margins strongly revolute and cartilaginous, the blade thick and leathery, nearly flat or characteristically strongly concave beneath, upper surface glossy and glabrous or a few stellate hairs persisting along the midrib near the base, lower surface (midrib and some veins excepted) densely and permanently fulvous or gray pubescent with a mixture of simple or branched puberulence and spreading stellate hairs; veins about 10 on each side with occasional intermediates, much branched and obviously anastomosing, markedly impressed above, very prominent (including the reticulum) beneath; petioles 3 to 10 mm long, stellately fulvous-glandular-pubescent. Staminate catkins about 4 to 6 cm long, rather loosely flowered, the peduncles glandular-pubescent, the hairy anthers at length exerted from the sparsely pubescent and ciliate calyces. Pistillate catkins 1 to 10 cm long, 2- or many-flowered along the fulvous-tomentulose peduncle. Fruit usually geminate or rarely solitary or more numerous; cups 10 to 13 or 15 mm broad, 8 to 10 mm high, basally constricted, margins simple, scales imbedded in dense lanate tomentum, the elongate apices merely puberulent and dark red; acorns 15 to 20 mm long, 9 to 12 mm broad, narrowly ovoid to subfusiform, obtuse or acute, glabrous and dull brown, about one-third included.

Range.—Coastal plain, especially along the immediate coast, on sandy soil or pure deep sand, North Carolina to Florida and westward to Mississippi and possibly Louisiana.

Since both *Quercus geminata* and *Q. minima* occur on sand in Florida, it is to be expected that two so closely related species would hybridize freely. Specimens of marked intermediate character are indeed to be found, these often having the pubescence and veins of *Q. geminata* and the low stature and tendency toward leaf toothing of *Q. minima*. The relative scarcity of such intermediates would indicate that an effective barrier to free crossing exists. Specific cases of such hybridization are discussed under *Q. minima*.

Willdenow's description of *Quercus maritima* clearly excludes what is here known as *Q. geminata* by its reference to leaves glabrous on both surfaces. The original misidentification seems to date back to Chapman whose *Q. virens* var. *maritima* is described as having leaves concave. Since then Sargent and Trelease have applied the name *maritima* to forms of *Q. geminata*. Willdenow's *Q. maritima* is a member of the subgenus *Erythrobalanus*. It was based upon *Q. phellos* β *maritima* Michx. which was illustrated in the *Hist. Chenes Amer. Sept.* pl. 13, fig. 3, where the apical seta is clearly delineated. The type in the Michaux Herbarium at Paris is labelled *Q. phellos* β *viridis*. Authentic duplicates occur in the Willdenow Herbarium at Dahlem and at Kew. The Kew collection is a series of fragments of the types pre-

pared and annotated by Andres Michaux. Willdenow's herbarium contains in addition two specimens under *Q. maritima*, one of *Q. virginiana* and the other of *Q. hemispherica* Bartram (which his description fits). Since the type of *Q. phellos* β *maritima* is a form of *Q. hemispherica* still common on the Atlantic Coast of South Carolina (e.g., *C. H. Muller* 10459, 10460, 10461), this plant is *Q. hemispherica* var. *maritima* (Michx.) comb. nov.²

Specimens examined:

NORTH CAROLINA: Brunswick Co., *W. W. Ashe* s. n.; *E. J. Palmer* 39829; collector undetermined (Biltmore Herb.) 4450; New Hanover Co., *R. K. Godfrey* 4725; *T. F. Woods* s. n., collector undetermined, (Biltmore Herb.) 4453; county undetermined, *J. A. Harris* 19378.

SOUTH CAROLINA: Beaufort Co., *J. R. Churchill* 341; *J. H. Mellichamp* s. n.; *C. H. Muller* 9937, 9938; *C. S. Sargent* s. n.; Charlestown Co., *K. W. Hunt* 2823; *J. K. Small* and *L. M. Bragg* s. n.

GEORGIA: Coffee Co., *R. M. Harper* 2050; Glynn Co., *T. G. Harbison* 1325, 1331; *C. H. Muller* 9923, 9924, 9925; Irwin Co., *F. J. Hermann* 10062; McIntosh Co., *C. H. Muller* 9929; County undetermined, *T. G. Harbison* s. n.

FLORIDA: Alachua Co., *T. G. Harbison* 5351; Bay Co., *C. H. Muller* 9800; Brevard Co., *F. S. Blanton* 6301; *A. Fredholm* 5746; *C. H. Muller* 9887, 9888, 9891, 9892; Citrus Co., *O. Degner* 5175; Collier Co., *C. H. Muller* 9834; Colubia Co., *L. McCulloch* s. n.; *P. H. Rolfs* s. n.; De Soto Co., *C. H. Muller* 9832; Dixie Co., *C. H. Muller* 9825, 9826; Duval Co., *J. R. Churchill* s. n.; *A. H. Curtiss* 2597 and/or 4597 (*pro parte*, cf. also *Q. minima*), 4189, 4598, 5786; Flagler Co., *C. H. Muller* 9907, 9908; Franklin Co., *A. W. Chapman* s. n.; Drummond 31; *R. K. Godfrey* 54092; *C. H. Muller* 9805, 9806, 9807, 10260, 10270, 10275, 10276; Hernando Co., *C. H. Muller* 10294; Hillsborough Co., *A. P. Garber* s. n.; Highlands Co., *W. W. Ashe* s. n.; *T. G. Harbison* 4623, 4652, 4653; *J. K. Small* and *J. P. De Winkeler* 9039; Lafayette Co., *T. G. Harbison* 55, 4813; *E. J. Palmer* 27319; Lake Co., *G. V. Nash* 516, 1623, 2414 (type); Lee Co., *A. S. Hitchcock* 337; *H. N. Moldenke* 979, 1013; Leon Co., *Reese* 610; *A. Steward* s. n.; Levy Co., *C. D. Mell* s. n.; *Edw. Palmer* 7620; Liberty Co., *L. Hubricht* B2063; Manatee Co., *C. H. M. Barrett* s. n.; *J. H. Simpson* 57; Marion Co., *C. D. Mell* s. n.; *C. H. Muller* 9827, 9831; Martin Co., *C. H. Muller* 9883; *J. K. Small*, *J. W. Small* and *J. P. De Winkeler* 10707; Okaloosa Co., *C. H. Muller* 9781; *Wakely* s. n.; Okeechobee Co., *J. K. Small*, *N. L. Britton*, *E. G. Britton* and *J. P. De Winkeler* 9251C; Orange Co., *T. G. Harbison* 3783; Pasco Co., *H. O'Neill* s. n.; Pinellas Co., *F. Beckwith* 609; Polk Co., *W. W. Ashe* s. n.; *J. Donnell Smith* s. n.; *T. G. Harbison* 3; *C. H. Muller* 10297; Putnam Co., *C. H. Muller* 10310, 10465, 10470, 10472; Seminole Co., *S. Rapp* 7, 12, 13, s. n.; St. Johns Co., *A. H. Curtiss* 6427; *C. H. Muller* 9920; *A. Ruth* s. n.; *G. B. Sudworth* s. n.; *C. S. Williamson* s. n.; St. Lucie Co., *J. A. Harris* 21127; *A. H. Howell* 1026; *C. H. Muller* 9884; *J. K. Small* and *J. P. De Winkeler* 9489; Taylor Co., *C. H. Muller* 9822, 9823; Volusia Co., *C. H. Muller* 9896; Wakulla Co., *C. H. Muller* 9810; Walton Co., *C. H. Muller* 9783, 9787, 9788, 9789, 9791, 9795, 9796; County undetermined, *A. W. Chapman* s. n.; *A. H. Curtiss* s. n.; *J. A. Harris* 21221; *F. Rugel* 98, 342, s. n.; *J. Schneck* 422, 424; *B. C. Tharp* 5404.

² *Quercus phellos* β *maritima* Michx., *Hist. Chenes Amer.* Sept. pl. 13, fig. 3. 1801.

ALABAMA: Baldwin Co., *D. Demaree* 35890, 35896, 35935, 35959, 35960, 35965; Mobile Co., *C. Mohr*, s. n.

MISSISSIPPI: Harrison Co., *D. Demaree* 33674, 33675, 35087, 35814, 35818; *T. G. Harbison* 3656, 3659; *C. H. Muller* 9764, 9765, 9983, 9984, 9985, 9986, 9987, 10000, 10001, 10002, 10005, 10006; *C. L. Pollard* 1054; *W. D. Sterrett* 1, 4, 5; *S. M. Tracy* and *F. E. Lloyd* 2, 3; *S. M. Tracy* 5138, s. n.; Jackson Co., *D. Demaree* 33568, 33892, 33899, 33970, 34093, 34105, 34519; *C. Mohr* s. n.; *C. H. Muller* 9957, 9959, 9960, 9961, 9962, 9971, 9972, 9979, 9981, 9982.

LOUISIANA: St. Martin Parish, *A. B. Langlois* 13.

6. *Quercus oleoides* Schl. and Cham., *Linnaea* 5:79. 1830.

Q. lutescens Mart. & Gal., *Acad. Brux. Bul.* 10:219. 1843.

Q. retusa Liebm., *Overs. Danske Vidensk. Selsk. Forhandl.* 1854:187. 1854.

Q. tropicae Berl., *Soc. Mex. Geogr. y Estad. Bol.* 5:128. 1857 (nom. nud.).

Q. oleoides var. *australis* Trel., *Mem. Nat. Acad. Sci.* 20:114. 1924.

Q. oleoides f. *lutescens* Trel., *Mem. Nat. Acad. Sci.* 20:114. 1924.

Small or large tree with spreading crown and rough hard dark bark. Twigs 1 to usually 2 to 3 mm in diameter, moderately or densely fulvous-glandular, puberulent or tomentulose with a mixture of simple and stellate hairs, at length glabrate or persistently pubescent. Buds about 2 to 3 mm long, subglobose or angular, glabrous and glossy dark red or gray-puberulent; stipules subulate, pubescent, quickly caducous. Leaves evergreen, rather thick and coriaceous, 4 to 10 or even 14 cm long, 2.5 to 5 or 7.5 cm broad, apically obtuse or sometimes acute or rounded or even retuse, basally cuneate, obovate to oblong or broadly oblanceolate, entire or exceptionally coarsely toothed especially above the middle, upper surface glossy and glabrous except the densely stellate-tomentulose midrib near the base, lower surface (except for the midrib and principal veins) densely fulvous or silvery appressed-stellate-tomentulose and frequently with spreading stellate hairs in addition; veins about 5 to 7 on each side and with occasional intermediates, strongly branched and obviously anastomosing, inconspicuous above or sometimes impressed, rather prominent beneath, often including the reticulum; petioles 4 to 10 or 12 mm long, densely fulvous-puberulent. Staminate catkins about 4.5 to 5.5 cm long, the peduncle fulvous-pubescent and moderately densely flowered, the markedly pubescent anthers well exerted from the very sparsely pubescent calyx. Pistillate catkins 1 to 6 cm long, 1- to several-flowered, the peduncle fulvous-glandular-tomentulose. Fruit solitary or paired; cup 12 to 15 or rarely 20 mm broad, 8 to 12 or rarely 20 mm high, deeply goblet-shaped, basally constricted, the scales sometimes markedly thickened basally, occasionally markedly vertically seriate, rather uniformly gray or silvery or tan pubescent throughout or the rather short apices less markedly so; acorn 20 to 25 mm long, 9 to 13 or rarely 16 mm broad, glabrous and rather dull brown, one-third or nearly one-half included.

Range.—Coastal plain and Piedmont, central Tamaulipas to Costa Rica, apparently confined to the Atlantic slope.

Quercus oleoides has a fairly wide tolerance of soil types. Although it is found on gravelly clay soils over much of its range, in coastal

Tamaulipas and adjacent Veracruz it occurs extensively on both clays and deep sands. The young plants are clearly rhizomatous and form small clumps prior to the assumption of tree form. The presence of spreading stellate hairs on the lower leaf surface and the occasional impression of the veins on the upper surface are characters of *Q. geminata* derived through the Cuban *Q. oleoides* var. *sagraeana*. These are encountered in *Q. oleoides* principally in the Veracruz population and scarcely appear below the Yucatan Peninsula. Conversely, the vertically seriate cup scales characteristic of a portion of the Veracruz population are observed occasionally in the Cuban variety and less frequently elsewhere.

Specimens examined:

MEXICO: Chiapas, *J. Bermudez* 2255, 2257, 2261, 2266; *M. Martinez* 374, 375, 387; *E. Matuda* 3732; *F. Miranda* 7201; Hidalgo, *H. E. Moore, Jr.* 3010; Oaxaca, *C. Conzatti* 3845; *L. S. Hernandez* 2260; *T. MacDougall* 2445, 2533, 2550; *M. Martinez* 690; *C. D. Mell* 27; *C. H. Muller* 9743, 9744, 9748; Puebla, *H. Bravo* 2068, 2069, 2379; *C. H. Muller* 9722, 9723, 9724, 9725, 9726, 9727; San Luis Potosi, *M. T. Edwards* 562; *C. H. Muller* 9701, 9702; *L. M. Palafox* 2133; *J. Rzedowski* 6996; Tabasco, *E. Matuda* 3129; *J. A. Peralta* 2113; Tamaulipas, *L. Berlandier* 2194 (= 774) (type of *Q. tropicae*); *P. S. Martin* 047, 049, 114, 115; *C. H. Muller* 9479, 9480, 9481, 9482, 9691, 9692, 9693B, 9694, 9696, 9697, 9698, 9699, 9700; *Edw. Palmer* 220, 318; Vera Cruz, *E. A. Goldman* 727; *H. Le Sueur* 86; *F. Liebmann* 3528; *J. J. Linden* 26; *E. Matuda* 1453; *C. D. Mell s. n.*; *F. Miranda* 7108; *D. Mojica* 2176; *C. H. Muller* 9477, 9478, 9728, 9729, 9730, 9730A, 9733, 9734, 9735, 9736, 9737, 9738, 9740, 9742; *E. W. Nelson* 67, 80; *C. A. Purpus* 6166, *s. n.*; *C. J. W. Schiede* 14 (Cotype), *R. Vorrath* 2277, 2278, 2279; Yucatan, *T. J. Burrill* 26513; State undetermined, *L. Berlandier* 543 (*pro parte*, cf. also *Q. fusiformis*); *F. Liebmann s. n.*; *C. A. Purpus* 14245.

GUATEMALA: *H. H. Bartlett* 12112; *S. F. Blake* 7735; *O. F. Cook* and *R. F. Griggs* 318; *C. C. Deam* 159; *Friedrichthal s. n.*; *C. Galusser* 1; *H. Pittier* 1789, 1818.

BRITISH HONDURAS: *H. H. Bartlett* 11203, 11204, 11308, 11313, 11552, 11553, 11873, 11886, 12976, 12979; *P. H. Gentle* 2695, 3378, 3792, 4072, 4156, 4162; *C. L. Lundell* 4347, 6627, 6837, 6964; *Kinloch* 97; *H. O'Neill* 8554, 8555; *W. A. Schipp* 209, 672.

HONDURAS: *P. H. Allen* 3887; *J. B. Edwards* 323, 375, 578; *A. Molina R.* 5, 7, 16, 492; *S. J. Record* and *H. Kuylen* 53, 53A; *P. Shank* 10782; *P. C. Standley* 861, 1356, 1366; *P. C. Standley* and *P. Chacon* 5684; *P. C. Standley* and *H. O. Lindellie* 7302; *C. Thieme* 5615; *W. von Hagen* and *C. von Hagen* 1095; *H. N. Whitford* and *L. R. Stadtmiller* 41, 55; *L. O. Williams* and *A. Molina R.* 10046, 10054, 11030, 12259; *T. G. Yuncker*, *J. M. Koepper* and *K. A. Wagner* 8179.

COSTA RICA: *A. M. Brenes* 15590; *C. W. Dodge* and *W. S. Thomas* 6232; *H. Pittier* 2127, 2607 (isotype of *Q. oleoides* var. *australis*).

6a. *Quercus oleoides* var. *sagraeana* (Nutt.) C. H. Mull., comb. nov.

Q. sagraeana Nutt., *Sylva* 1:17. 1842.

Q. cubana Richard, *Fl. Cuba* 3:230. 1853.

Q. virginiana var. *sagraeana* Trel., *Mem. Nat. Acad. Sci.* 20:113. 1924.

Small or large trees with spreading crowns and rough gray or dark bark. Twigs 1.5 to 2.5 mm in diameter, persistently fulvous-glandular-

tomentulose or at length glabrate. Buds about 2 mm long, subglobose or obscurely round-angled, dark red, sparsely puberulent; stipules subulate, pubescent, quickly caducous. Leaves evergreen, hard and coriaceous, 3 to 9 cm long, 1 to 3.5 cm broad, oblong to obovate or broadly oblanceolate, acute to obtuse or even broadly rounded, entire or frequently coarsely and irregularly toothed, the margins strongly revolute, the blade nearly flat or markedly concave, upper surface glabrous and glossy except the persistently stellate-pubescent midrib and principal veins, lower surface characteristically minutely dense-tomentulose with a mixture of simple and stellate appressed hairs, fulvous-glandular or silvery, but commonly also with spreading stellate tawny hairs, the midrib and principal veins nearly glabrous; veins 8 or 9 on each side, strongly branched and obviously anastomosing, rather markedly impressed above, very prominent (including the reticulum) beneath; petioles 2 to 10 mm long, densely fulvous-tomentulose. Staminate catkins about 5 cm long, rather loosely flowered, the pubescent anthers little exerted. Pistillate catkins 1 to 3 or 4 cm long, 2- or 3-flowered on a fulvous-tomentulose peduncle. Fruit solitary or paired, the coarse peduncle fulvous-tomentulose; cup 12 to 20 mm broad, 10 to 20 mm high, deeply cup-shaped, basally usually markedly constricted, the scales basally thickened and densely fulvous-tomentose, the dark red apices thin and puberulent; acorn about 20 to 25 mm long, 12 to 15 mm broad, ovoid, glabrous and dull or glossy brown, about one-third included.

Range.—Coastal plain and uplands of the Pinar del Rio province, Cuba.

The forms of *Quercus oleoides* var. *sagraeana* with plane leaves, less prominent veins, and lacking the loosely spreading stellate hairs on the lower surface are usually characterized by fruits in which the cup scales are strongly seriate as in much of *Q. oleoides*. Those foliage specimens most suggestive of *Q. geminata*, on the other hand, are associated with cups the scales of which are not markedly seriate and which might readily be accepted within *Q. geminata*. The population, although somewhat variable, is rather well distinguished from *Q. oleoides* by shape, concavity, venation, and pubescence of the leaves and from *Q. geminata* by the mitigation of these characters with the flat blades, short pubescence, and inconspicuous veins of *Q. oleoides*. The origin of the variety as a hybrid swarm of *Q. oleoides* and *Q. geminata* is clearly indicated by this mixture of characters (Muller, 1955). The present disposition of this entity as a variety of *Q. oleoides* is dictated by its somewhat greater richness in the characters of that species than in those of *Q. geminata*. Contrary to the opinion of Trelease, there is no indication of relation with *Q. virginiana* in any part of the insular population.

Specimens examined:

CUBA: Pinar del Rio: N. L. Britton, E. G. Britton and J. F. Cowell 9650, 10108; N. L. Britton, E. G. Britton and C. S. Gager 7304, 7305; N. L. Britton and F. S. Earle 6580; M. T. Cook 15, 16, 17, 18, 19, 20, 21, 22, s. n.; F. S. Earle s. n.; V. Hermann 813, 3324, 7561; V. Hermann and Munz s. n.; E. P. Killip 13564; Bro. León 4251; Bro. León and Bro. M. Roca

6990; C. H. Muller 9835, 9836, 9837, 9838, 9839, 9840, 9841, 9842, 9843, 9844, 9845, 9846, 9847, 9848, 9849, 9850, 9851, 9852, 9853, 9854, 9855, 9856, 9857, 9858, 9859, 9860, 9861, 9862, 9863, 9864, 9865, 9866, 9867, 9868, 9869, 9870, 9871, 9872, 9873, 9874, 9875, 9876, 9877, 9878; O'Donovan 1000; W. Palmer and J. H. Riley 432; L. R. Rivas 21996; R. de la Sagra s. n. (isotype of *Q. sagraeana* and *Q. cubana*); J. A. Shafer 11035, 11906, 11908, 11910; J. A. Shafer and Bro. León 13676; C. Wright 698, 2292.

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Normal Heteromorphism in Earthworms¹

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ABSTRACT: Normally organized heteromorphic regenerates mentioned in the literature are of four species. Heteromorphic heads and tails from *Perionyx sansibaricus* and *Ocnerodrilus occidentalis*, as well as a heteromorphic tail from *Gordiodrilus peguanus*, are recorded. A heteromorphic head was developing at 47/48 on a specimen of the common lumbricid *Allolobophora tuberculata*. The pre-intestinal region is able, regardless of direction, to regenerate only a head or some portion of one. The intestinal region can regenerate heads as well as tails and at certain levels one or the other as determined by unknown factors of internal environment.

Anterior heteromorphism, a tail regenerated instead of a head, was discovered by Bonnet in oligochaetes (possibly including some earthworms) as long ago as 1745. Posterior heteromorphism, a head regenerated instead of a tail, was not recognized in earthworms until around 1925. Heteropolar growths may be monstrous in various ways, or a regenerate may be heteromorphic only in part and then also in different ways. Normal regenerates, *i.e.*, solely cephalic or caudal, with normal metamerism, and lacking outgrowths or other aberrations, have been recorded in the literature from four species of earthworms, as follows:

Criodrilus lacuum, European, with segments to 450. One heteromorphic head (Janda, 1926) of 16 segments at intersegmental furrow 22/23, a head of 20 and another of 23 segments at unknown levels. Heteromorphic tails rarely were obtained and then only from adults. No data were published as to kind of operation, level of regeneration or number of segments in regenerates. These heteropolar tails may have been produced by fragments with two cut surfaces as in *Eisenia foetida* or by short terminal portions as in species of *Perionyx*.

Eisenia foetida, of European origin but widely distributed in America, with 100-125 segments. Heteromorphic tails (Gates, 1949) regenerated at levels 20/21-54/55, number of segments increasing to a maximum of 25 at 40/41 and then decreasing. Heteromorphic tails (Gates, 1950b) also were regenerated by fragments of various sizes cut out from a middle portion of the body. Regeneration of heteromorphic heads (Gates, 1950a) is probable, in favorable conditions, at levels 16/17-34/35.

Perionyx excavatus, of Himalayan origin but now widely distributed in the tropics, with 100-200 segments. Heteromorphic head regeneration (Gates, 1927, 1941, 1943) possible at 12/13-27/28 and has been induced merely by a simultaneously made second transection at subsequent levels back to 68/69. Heteromorphic tails regen-

¹ From a manuscript written during tenure of a John Simon Guggenheim fellowship.

erated only by terminal portions comprising the last 42 or fewer segments. Data as to number of segments in heteropolar tails and in some of the heteromorphic heads no longer are available.

Perionyx millardi, endemic in peninsular India, with segments to 220. Heteromorphic heads regenerated at 7/8-22/23 (Gates, 1951) and after induction by a second transection at subsequent levels back to 88/89. Number of segments in these heteromorphs varied from 2-15, at 17/18 for instance and under uniform external conditions from 6-15, the maximum number obtained at several of the levels 17/18-31/32. Heteromorphic tails were regenerated by substrates comprising the last 44-17 segments, also by small fragments cut out from a posterior region of the body. Maximum number of segments 15, however usually only 1-5. All experimentally obtained regenerates in this species were provided by juvenile worms as adults were unobtainable. Heteromorphism occasionally found in natural regenerates was not normal.

Normal heteromorphism now can be recorded from three further species of earthworms. The procedures utilized have been described previously (Gates, 1927).

Perionyx sansibaricus, originally from peninsular India but now domiciled elsewhere in the tropics, with segments to 200. Heteromorphic heads regenerated at 7/8-20/21 and after induction by a simultaneous second transection at subsequent levels back to 50/51. Number of segments, 3 at 7/8, 6 and 8 at 8/9, 4-10 at 9/10, 7-15 at 20/21, 7-13 at 32/33. Heteromorphic tails were regenerated at levels 75/76-185/186, the substrates comprising the last 91-15 segments of the body. Number of segments, 2-8. Number of segments in heteromorphic tails regenerated by fragments cut out of the posterior portion of the body so as to contain the fifteen segments immediately in front of the last fifteen, 2-20. These results were obtained from operations on adult animals.

Gordiodrilus peguanus, peregrine and widely distributed in the tropics but presumably of African origin, possibly with 80-100 segments. One heteromorphic tail of 16+ segments at 16/17. Metameric differentiation had not been completed at time of preservation. The clitellum was still recognizable on segments xvii-xviii of the substrate and appeared to have undergone no regression during the two or more weeks required for formation of the regenerate.

Ocnodrilus occidentalis, peregrine and widely distributed in temperate zones as well as in the tropics but presumably of American origin, with 70-84 segments. All regenerates from adults.

Heteromorphic heads of 6-7 segments regenerated at 19/20. Other posterior regenerates at the same level were cephalocaudal monstrosities or homomorphic tails. All posterior regenerates at levels 20/21-34/35 were normal homomorphic tails.

Heteromorphic tails at 21/22, at time of preservation, had not yet completed metameric differentiation though a number of segments already were demarcated and provided with setae. Other anterior

regenerates at 21/22 were monstrous. At 19/20 all anterior regenerates were monstrous, usually in part cephalic. All anterior regeneration at 12/13 was homomorphic. The maximum number of segments in those head regenerates was 10.

Worms of the above experiments had been fasted for a day or two before operating. Specimens of *O. occidentalis*, starved for several weeks before the operations, failed to regenerate though surviving long enough (3 weeks) to have done so.

Probability of normal heteromorphosis in another species of the same family as *E. foetida* also can be recorded.

Allolobophora tuberculata, of European origin but now widely distributed in other parts of the world, with 146-194 segments. A natural posterior regenerate at 47/48 might have become normally heteromorphic if development had been completed in the only direction that was morphologically recognizable. Unfortunately, feeding had continued after amputation and accumulations of ingested soil had ruptured the regenerate proximally just as the worm was found. Five segments already had been marked off externally on the regenerate. A pharyngeal bulb had been formed in the gut. The nerve cord terminated well away from distal end of regenerate in a sub-pharyngeal ganglion. The brain and circumpharyngeal commissures had not yet been formed. The distal end of the regenerate had the shape of a cephalic rather than a caudal growth but indications of prostomial sculpturing and buccal invagination had not become recognizable. The last two substrate segments had been considerably elongated. The epidermis and musculature had acquired a different appearance and texture indicative of histological changes. Setae of the 47th segment had been dehiscent. Apertures of setal follicles had disappeared, leaving no recognizable traces of their former locations. Setal follicles apparently had been completely histolyzed. These are just the morphallactic changes sometimes associated, in better known species of earthworms, with head regeneration.

This regenerate, as well as the heteromorphic heads obtained at 32/33 and 34/35 in *E. foetida*, requires re-evaluation of results of various experiments on morphogenesis in earthworms. The regenerate also enables the following predictions. Homomorphic head regeneration will be obtainable, without special difficulty, in the pre-intestinal region of *A. tuberculata* and more rarely but only in conditions presently unknown at subsequent levels back to 47/48 at least. Equimeric heads will be regenerated at least at all levels back to 5/6, possibly even to 8/9 or 9/10.

DISCUSSION

Worms with heteromorphic regenerates are, of course, doomed to die from starvation or constipation unless some way is found to enable feeding or defecation. Although the enteric lumen is continuous from mouth to mouth in a two-headed individual, matter apparently can pass only in one direction, at least through a distal portion of the gut. Hence, ingesta accumulate until the mass is sufficient to rupture gut

and body wall. Even if the animal fasts, enteric secretions and especially calcareous concretions may burst out through substrate or regenerate. Individuals that were ruptured in the laboratory usually did not survive, even in hardy species with unusually high regenerative capacity. Greater viability in nature is not to be expected judging from rarity of heteromorphism in conditions resulting in frequent regeneration. Morphological regularization of heteromorphosis so as to permit feeding or defecation and presumably viability sometimes does take place, in nature as well as in the laboratory. The various sorts of regularization will be considered, circumstances permitting, in a subsequent communication.

Although only one kind of heteromorphism is known presently in two species, the other sort doubtless will be found. Heteropolar heads and tails have been found in six species of four families. Information as to heteromorphosis that is now available for four of the species warrants the following generalizations. The pre-intestinal region of the body, herein called head though that term sometimes has had a much more restricted meaning, is able to regenerate only a head or some portion of one. The intestinal region of the body is able to regenerate heads as well as tails and at certain levels one or the other as determined by unknown factors of internal environment. Similar regenerative capabilities are likely in the other four species.

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Early Development of the Secondary Bronchi in the House Sparrow *Passer domesticus* (Linnaeus)¹

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ABSTRACT: This study presents the origin, development and relationships of the secondary bronchi in the embryo of the House Sparrow, *Passer domesticus* (Linnaeus). Serial transverse, frontal or sagittal sections at six or eight microns were made of one or more embryos, fixed in Bouin's or Lavdowsky's fluid, embedded in paraffin and stained with Delafield's Hematoxylin, for each half-day interval from two through nine days incubation. Photomicrographs, camera lucida tracings, direct projections were used to make diagrammatic reconstructions at regular intervals of incubation.

The time and point of origin and general destination of each secondary bronchus is described. Three groups of secondary bronchi occur in this species. The five *mesiobronchi* arise on the dorsal, dorsomesial or dorsolateral surface of the mesobronchus and occupy the anteromesial and mesial regions of the lung. The nine *dorsobronchi* arise on the dorsal and dorsolateral surface of the mesobronchus and occupy the anterodorsal, dorsal and dorsolateral regions of the lung. The nine *lateroventrobronchi* arise on the lateroventral and lateral surfaces of the mesobronchus and occupy the ventral and lateroventral portions of the lung.

Detailed description is given for the development of the mesobronchus, secondary bronchi and tertiary bronchi concerned with the origin of the individual airsacs. Primary and secondary ostia of the intermediate and anterior abdominal airsacs are described. Migration of origins or mouths of secondary or tertiary bronchi from the lung to the airsac side of an airsac ostium are given for the intermediate, anterior abdominal and posterior abdominal airsacs.

The individual secondary bronchi are compared with those described in other species. The time of origin of the secondary bronchi in the House Sparrow are compared with those of the chicken; these structures appear earlier in the House Sparrow than in the chicken.

INTRODUCTION

Literature reviews on the structure of the respiratory system of Aves can be found in the works of Sappey (1847), Roche (1891), Baer (1896), Moser (1902), Bertelli (1905), Fischer (1905), Muller (1908), Schulze (1912), Juillet (1912), and Locy and Larsell (1916).

Selenka (1866) described the development of the airsacs in chickens. Locy and Larsell (1916) described in more detail the development of the lungs and airsacs in the domestic fowl. Bertelli (1905) and Poole (1909) discussed the diaphragmatic tissue in its relation to the development of the lungs and airsacs.

The present investigation describes the origin and location of

¹ Published in partial fulfillment of requirements for Ph.D. degree, University of Nebraska; University of Nebraska Department of Zoology Publ. No. 321.

the secondary bronchi in the embryo of *Passer domesticus* (Linnaeus), the house sparrow. The adult airsacs of this species have been figured grossly by such workers as Fischer (1905), Juillet (1912) and Wetherbee (1951).

Acknowledgments.—The writer expresses his thanks to his advisor, Dr. Otis Wade, Prof. Emeritus, University of Nebraska for guidance in this study. Acknowledgment is made to the North Dakota Institute of Regional Studies for financial support and to the Departments of Zoology and Veterinary Science for facilities used in this study.

MATERIALS AND METHODS

Embryos of the house sparrow were fixed in Bouin's fluid or Lavdowsky's fluid. Histological sectioning was performed using the di-oxan-paraffin technique. Seventy per cent acid alcohol was used to soften older embryos. Serial sections of embryos were made at each half-day interval from two through thirteen days incubation (hatching time). Transverse, frontal and sagittal sections were used. Sections varied in thickness from six microns for the younger embryos to twenty microns for the embryos near and at hatching time. The lungs of several adults were sectioned between 10 and 20 microns. All staining was done with Delafield's hematoxylin.

Representative tracings and occasional photomicrographs from the various serially sectioned embryos were used in making diagrammatic reconstructions of the lungs, airsacs and airsac diverticula. Such reconstructions were made from frontal, lateral and mesial views.

OBSERVATIONS

The early stages of development of the lungs of the house sparrow are similar to that described for the chicken by Selenka (1866), Bertelli (1905), Poole (1909) and Locy and Larsell (1916) (Figs. 1, 2, 3, 4).

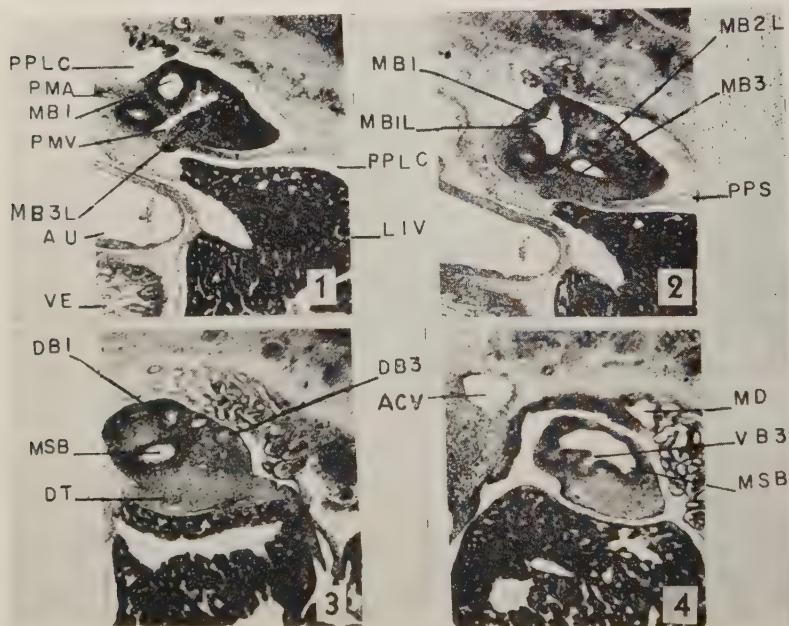
THE PRIMARY BRONCHUS

The primary bronchus enters the lung near its mesioventral apex. This bronchus is called the mesobronchus after it enters the lung (Huxley, 1882). A gradual shift of the entrance of the primary bronchus is apparent from three through nine days incubation. The final position of the point of entrance is the center of the mesial apex of the lung. The mesobronchus extends through the lung as a dorso-lateroposterior continuation from its point of entrance. During the third day of incubation this tube becomes curved in three different regions: 1) the proximal end curves dorsoposteriorly and expands into the embryonic vestibulum; 2) the embryonic vestibulum projects sharply dorsally and laterally toward the dorsal floor of the lung; 3) the postvestibular mesobronchus turns sharply posteriorly and projects along the dorsolateral lung margin toward the posterior tip of the lung. This portion of the mesobronchus progressively diminishes in diameter from the embryonic vestibulum to the posterior limit of the mesobronchus which is curved mesially and ventrally (Fig. 5).

The posterior end of the mesobronchus pushes out of the lung slightly anterior to its posterior tip and ventral to its dorsal border by five days incubation. The projection of the mesobronchus beyond the lung wall into the pleuroperitoneal cavity constitutes the origin of the primordium of the *posterior abdominal airsac*.

THE SECONDARY BRONCHI

The primary bronchus of the embryo gives rise to twenty-three subdivisions of varying dimensions, the secondary bronchi. Each sec-



Figs. 1-4.—Sagittal sections of embryos of *Passer domesticus* at four and one-half days incubation: right lung sectioned at six microns; 100 magnifications. 1. Section through mesial area of lung showing entrance of pulmonary vein. 2. Section 50 microns lateral to Figure 1 showing entrance of primary bronchus into the lung. 3. Section 50 microns lateral to Figure 2 showing mesial extensions of dorsobronchi 1, 2, and 3. 4. Section 50 microns lateral to Figure 3 showing origins of lateroventrobronchi 2 and 3.

Abbreviations: ACV, anterior cardinal vein; AU, auricle; DB1, dorso-bronchus number one; DB3, dorsobronchus number three; DT, diaphragmatic tissue; LIV, liver; MBI, mesibronchus number one; MB1L, lateral ramus of mesibronchus number one; MB2L, lateral ramus of mesibronchus number two; MB3L, tertiary bronchus of mesibronchus number three (MB3L is ICIM prior to the existence of the latter in the tissue outside the lung); MD, mesonephric duct; MSB, mesobronchus; PMA, pulmonary artery; PMV, pulmonary vein; PPLC, pleuroperitoneal cavity; PPS, pleuroperitoneal septum (synonym of diaphragmatic tissue); VB3, lateroventrobronchus number three; and VE, ventricle.

ondary bronchus, large or small, gives rise to subdivisions. The monopodial and dichotomous systems of branching of His (Locy and Larsell, 1916) are shown by the secondary bronchi in this species. This can be exemplified by a description of some of the ramifications of the most anterior secondary bronchus or first mesiobronchus. Numerous small subdivisions arise along the dorsal surface of the secondary bronchus in the monopodial fashion; the branches are smaller than the main trunk and are given off without a decrease in the size of the main trunk. Some of these tertiary bronchi are divided monopodially but many of them show bifurcations of equal dimension at their distal end. These quaternary bronchi originate in a dichotomous fashion. Subdivisions have been observed through the fifth and sixth order of bronchial branching. By the eleventh day of incubation the secondary, tertiary, quaternary, and lesser bronchi show a further subdivision in the form of small air capillaries which arise as projections from the secondary bronchi and other lesser bronchial subdivisions. Anastomoses of tertiary bronchi or bronchi of fourth, fifth or sixth order take place throughout the lung by the completion of ten days incubation. The more minute air passages also anastomose freely.

The secondary bronchi can be placed in three groups:

1. Mesiobronchi—bronchi which send tributaries over the mesial surface of the lung.
2. Lateroventrobronchi—bronchi which traverse the lateral and ventral area of the lung.
3. Dorsobronchi—bronchi which penetrate the lung mesoderm through most of the dorsal area of the lung.

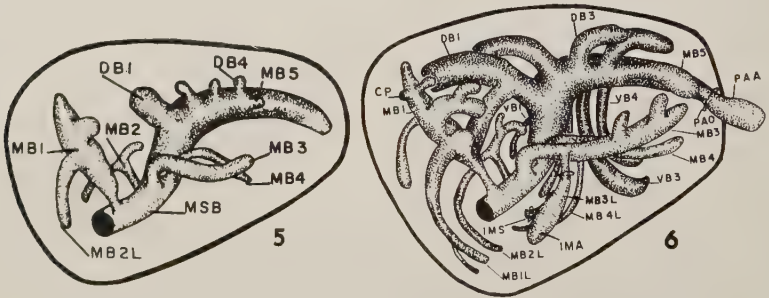
THE MESIOBRONCHI

The First Mesiobronchus (first entobronchus of Locy and Larsell, 1916).—This is the most anterior secondary bronchus and also the first to appear in the house sparrow in point of time. This secondary bronchus originates at about three days incubation as a projection from the dorsomesial surface of the mesobronchus immediately distal to the entrance of the primary bronchus into the lung (Fig. 5), and reaches the anterodorsomesial tip of the lung by three and one-half days incubation. At this time it has given off a large tertiary bronchus on its anteromesial margin about midway along the length of the secondary bronchus. This tertiary bronchus grows until it reaches the anteromesial border of the lung and then turns lateroventrally. By four and one-half days incubation the distal limit of this tertiary bronchus (the first lateroventral ramus) has reached its definitive position dorsal to the lateroventral apex of the lung and anteroventromesial to the lateroventral ramus of the second mesiobronchus (Fig. 6). An important quaternary bronchus arises at five days incubation on the lateroventral surface of the first lateroventral ramus and travels laterally and anteriorly to the lateroventral ramus. This quaternary

bronchus is the forerunner of the *lateral moiety* of the *interclavicular airsac*.

Numerous smaller tertiary bronchi appear along the dorsal and ventral surface of the secondary bronchus by six and one-half days incubation. All the tertiary bronchi of the first mesio-branchus occasionally divide dichotomously at their distal limits, but the more frequent method of subdivision is that of a lateral projection from the main axis of the bronchus (monopodial method). They develop quaternary subdivisions in monopodial and dichotomous fashion throughout their length.

At about five and one-half days incubation an anteriorly directed tertiary bronchus arises on the anterior surface of the first mesio-branchus a short distance proximal to the distal tip of the secondary



Figs. 5-6.—Diagrammatic reconstruction (mesial view) of bronchial ramifications in the right lung of embryos of *Passer domesticus* at various ages. 5. Four days incubation. 6. Five and one-half days.

Abbreviations: AAA, anterior abdominal airsacs; AASO, orifice of secondary ostium of anterior abdominal airsac; CA, cervical airsac; CAO, orifice of cervical airsac; CP, tertiary bronchus giving rise to cervical airsac; DB1, dorsobronchus number one; DB3, dorsobronchus number three; DB4, dorsobronchus number four; DB5, dorsobronchus number five; DB6, dorsobronchus number six; DB7, dorsobronchus number seven; DB9, dorsobronchus number nine; ICA, mesial moiety of interclavicular airsac; ICLMP, quaternary bronchus which originates lateral moiety; IMA, intermediate airsacs; IMS, secondary ostium of intermediate airsac; IMT, tertiary ostium of intermediate airsac; MB1, mesio-branchus number one; MB1L, lateral ramus of mesio-branchus number one; MB2, mesio-branchus number two; MB2L, lateral ramus of mesio-branchus number two; MB3, mesio-branchus number three; MB3L, tertiary bronchus of mesio-branchus number three (MB3L is ICIM prior to the existence of the latter in the tissue outside the lung); MB4, mesio-branchus number four; MB4L, lateral ramus of mesio-branchus number four; MB5, mesio-branchus number five; MSB, mesio-branchus; PAA, posterior abdominal airsac; PAO, orifice of posterior abdominal airsac; VB1, lateroventrobronchus number one; VB1A, anterior ramus of lateroventrobronchus number one; VB1V, ventral ramus of lateroventrobronchus number one; VB2V, ventral ramus of lateroventrobronchus number two; VB3, lateroventrobronchus number three; VB4, lateroventrobronchus number four; VB6, lateroventrobronchus number six; VB8, lateroventrobronchus number eight; and VB9, lateroventrobronchus number nine.

bronchus. This structure pushes against the lung wall and projects as a thumb-like bulge into the pleuroperitoneal cavity by six days incubation. This is the primordium of the *cervical airsac*.

The Second Mesiobronchus (second entobronchus of Locy and Larsell, 1916).—This structure arises between three and three and one-half days incubation as an anterodorsal projection from the dorso-lateral surface of the mesobronchus immediately distal to the origin of the first mesiobronchus. The secondary bronchus bifurcates distally into two tertiary rami.

The mesioposterior ramus travels toward the mesial lung border where its distal end takes its place posterior to the most proximal of the mesioposterior tertiary bronchi of the first mesiobronchus. The ramus gives rise to tertiary bronchi in the same way and at the same time as does the first mesiobronchus.

The lateroventral ramus of the secondary mesiobronchus grows anteriorly, laterally and ventrally from its origin so that by five days incubation the distal end lies lateral, posterior and dorsal to the distal end of the lateroventral ramus of the first mesiobronchus.

The Third Mesiobronchus (third entobronchus of Locy and Larsell, 1916).—This bronchus originates during the fourth day of incubation as a dorsomesial projection from the mesial surface of the mesobronchus distal to the origin of the second mesiobronchus (Fig. 5). This branch turns sharply posteriorly and travels caudally along the mesial surface of the lung. Numerous large tertiary bronchi arise along the mesial surface and project dorsally and slightly posteriorly from four and one-half through seven and one-half days incubation. Another group of tertiary bronchi arises along the ventral surface. These project lateroventrally over the mesioventral surface of the lung. Additional smaller tertiary bronchi are noticed along the dorsal margin of the secondary bronchus. The third mesiobronchus gives rise to a mesioventrally directed projection (a tertiary bronchus) arising at approximately four days incubation on the ventromesial surface, a short distance posterior to the posteriorly directed curvature of the third mesiobronchus. By four and one-half days incubation this tertiary bronchus has reached the lung surface and, distal to this point, curves anterolateroventrally to a point ventral and lateral and slightly posterior to the origin of the parent secondary bronchus. By five days incubation the lateral surface of this tertiary bronchus shows a small projection (quaternary bronchus) midway along its length. During the following twelve hours the proximal and distal extremities of the tertiary bronchus remain in the lung while the entire middle portion and the proximal portion of the quaternary bronchus become located in the diaphragmatic tissue on the mesial surface of the lung; the tertiary bronchial portion outside the lung swells in diameter progressively from the proximal end. The distal portion of the tertiary bronchus now lying outside the lung is the *primordium* of the *mesial moiety* of the *interclavicular airsac* and the *intermediate airsac*. The primordium thus possesses a primary or proximal and a secondary or distal

ostium derived from the original tertiary bronchus plus a tertiary ostium or auxiliary connection derived from the laterally projected quaternary bronchus (Fig. 7).

The Fourth Mesiobronchus (fourth entobronchus of Locy and Larsell, 1916).—This structure arises at three and one-half days incubation as a projection from the anteromesial surface of the mesobronchus posterior to the origin of the third mesiobronchus. During the following twelve hours this branch turns dorsomesially and continues toward the mesial surface of the lung. This bronchus curves sharply posteriorly and travels lateroposteroventrally along the posterior portion of the mesial surface of the lung during the following two days incubation. The fourth mesiobronchus lies lateral and ventral to the posterior projection of the third mesiobronchus. Near its mouth, the fourth mesiobronchus gives rise to a ventrally directed tertiary bronchus which travels laterally and posteriorly to the similar tertiary bronchus of the third mesiobronchus.

The Fifth Mesiobronchus (the fifth ectobronchus of Locy and Larsell, 1916).—The fifth originates at about three and three-fourths days incubation as a mesioposterior projection from the mesial surface of the mesobronchus midway along the length of the posterior continuation, distal to the embryonic vestibulum. The secondary bronchus continues its growth posteriorly to the level of the three posterior lateroventrobronchi.

The fifth mesiobronchus is significant because the more posterior of

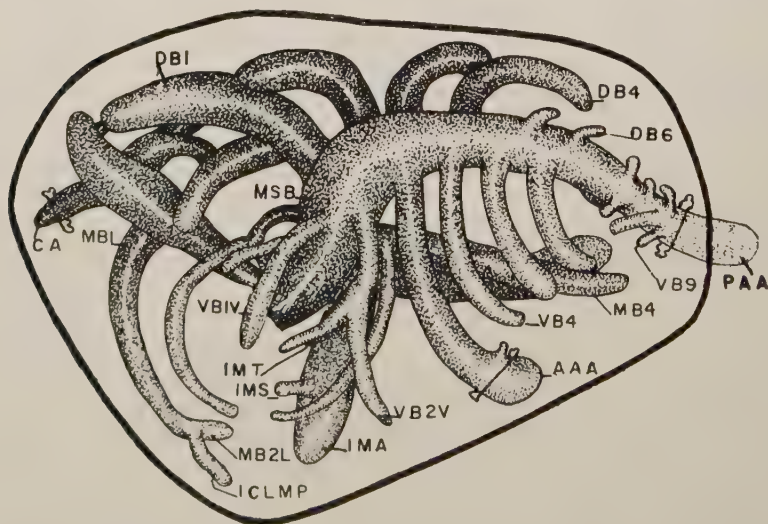


Fig. 7.—Diagrammatic reconstruction of bronchial ramifications in the left lung of an embryo of *Passer domesticus* after six days incubation; lateral view. For abbreviations see legend, Figs. 5 and 6.

the mesioposterior tertiary bronchi become associated with the distal ends of the three posterior dorsobronchi.

THE DORSOBRONCHI

The First Dorsobronchus (a ramus of the first ectobronchus of Locy and Larsell, 1916).—This structure originates by three and one-half days of incubation as a bulge on the anterior surface of the embryonic vestibulum immediately proximal to the posterior continuation of the vestibular region of the mesobronchus (Fig. 5). This secondary bronchus continues anterodorsomesially until it lies dorsal to the point of bifurcation of the second mesibronchus; from this position, it turns anteriorly and slightly laterally as it grows along the dorsal floor of the lung. The final position of the distal or anterior tip is lateral, dorsal and slightly posterior to the distal limit of the first mesibronchus.

The first dorsobronchus gives rise to a significant tertiary bronchus from its anteroventral margin, at the crest of the curvature described above, during the fifth day of incubation. This tertiary anterodorsomesial branch extends anterolateroventrally so that its subdivisions can anastomose with branches from the primordium of the lateral moiety of the interclavicular airsac by nine and one-half days incubation.

The Second Dorsobronchus (first ectobronchus of Locy and Larsell, 1916).—This bronchus originates by four days incubation as an anterodorsomesial protrusion from the anterodorsal surface of the mesobronchus distal to the origin of the first dorsobronchus. During the fifth day of incubation the second dorsobronchus curves dorsally and extends along the lateral surface of the anterior projection of the first dorsobronchus.

The Third Dorsobronchus (second ectobronchus of Locy and Larsell, 1916).—This structure appears during the fourth day of incubation on the dorsomesial surface of the mesobronchus posterior to the origin of the second dorsobronchus and on the opposite side of the mesobronchus from the origin of the third lateroventrobronchus. The third dorsobronchus projects toward the dorsomesial lung surface. It then turns posteriorly. The secondary bronchus comes to lie in its definitive position dorsomesial to the main mass of the fourth dorsobronchus during the sixth day of incubation.

The Fourth Dorsobronchus (third ectobronchus of Locy and Larsell, 1916).—The fourth originates at the same time as, and posterior to, the preceding dorsobronchus. The fourth dorsobronchus projects toward the dorsomesial surface of the lung and turns posteriorly to travel along the dorsal floor of the lung mesial to the mesobronchus and lateral to the posterior or distal continuation of the third dorsobronchus. Its distal limit lies dorsal to the distal extremity of the third mesibronchus. The fourth dorsobronchus has no direct relation to the airsacs.

The Fifth Dorsobronchus (sixth ectobronchus of Locy and Larsell, 1916).—This bronchus appears at approximately six days incubation as a projection from the dorsolateral surface of the mesobronchus

posterior to the origin of the fifth mesobronchus and dorsal to the origin of the sixth lateroventral bronchus. The fifth dorsobronchus turns posteriorly at the point where it approximates the dorsolateral margin of the lung and extends toward the posterior tip of the mesobronchus.

The Sixth Dorsobronchus (seventh ectobronchus of Locy and Larsell, 1916).—This structure originates at the same time and directly posterior to the fifth dorsobronchus. The growth and destination of the two bronchi are quite similar except for the fact that the sixth dorsobronchus does not extend as far posteriorly as the fifth dorsobronchus.

The Seventh Dorsobronchus.—This secondary bronchus has uncertain homology in the chicken as described by Locy and Larsell (1916). In the house sparrow, it originates by six days incubation on the dorsolateral surface of the mesobronchus proximal to the eighth and ninth dorsobronchi and extends dorsolaterally and anteriorly. The mouth or origin of the seventh dorsobronchus shifts to the 'airsac side of the ostium of the posterior abdominal airsac.

The Eighth Dorsobronchus.—The eighth occurs on the dorsolateral surface of the mesobronchus posterior to the orifice of the seventh dorsobronchus; the two originate at the same time. The eighth dorsobronchus travels laterally and anteriorly along the dorsolateral margin of the lung until its distal end comes to lie adjacent to the distal end of a tertiary bronchus from the sixth dorsobronchus. The mouth of the eighth dorsobronchus shifts to the airsac side of the orifice of the posterior abdominal airsac (Fig. 8).

The Ninth Dorsobronchus.—The ninth originates on the dorsolateral surface of the mesobronchus, dorsal and distal to the orifice of

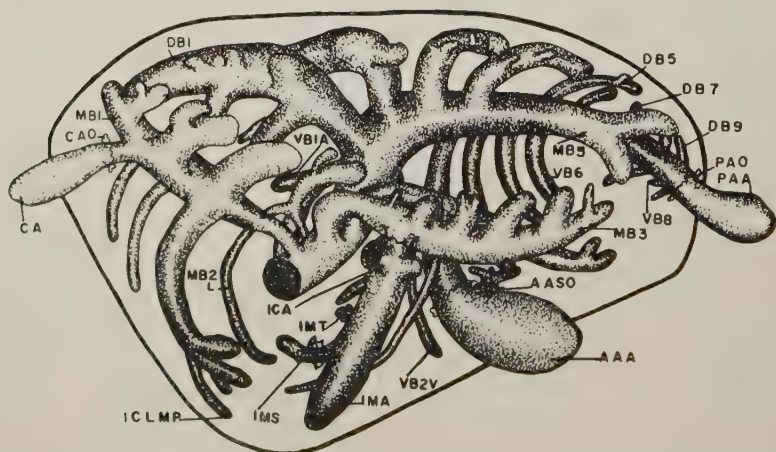


Fig. 8.—Diagrammatic reconstruction (mesial view) of representative tertiary and quaternary bronchi of right lung of an embryo of *Passer domesticus* at seven and one-half days incubation.

the preceding secondary bronchus, a few hours after the origin of the latter. The general destination of the ninth dorsobronchus is posterior, dorsal and slightly mesial to that of the eighth dorsobronchus. The mesial location is due to the curve in the mesobronchus proximal to the origin of the posterior abdominal airsac. The ostium of the ninth dorsobronchus precedes the ostia of the eighth and seventh dorsobronchi from the mesobronchus within the lung to the mouth of the airsac immediately outside the lung proper by the eleventh day of incubation.

The presence of the ostia of the three posterior dorsobronchi on the airsac mouth outside the lung by eleven days of incubation is similar and suggests a similarity to recurrent bronchi in other species (Juillet, 1912; Schulze, 1912; Locy and Larsell, 1916).

THE LATEROVENTROBRONCHI

The First Lateroventrobronchus (first laterobronchus of Locy and Larsell, 1916).—This structure arises at four days incubation on the anterolateral surface of the mesobronchus at the proximal limit of the embryonic vestibulum a short distance ventral and lateral to the origin of the first dorsobronchus. The structure bifurcates into a lateroventral and an anterolateral ramus by the completion of six days incubation. The former travels lateroventrally and slightly posteriorly until its distal end lies dorsal to the lateroventral margin of the lung. The latter lies dorsal, lateral and slightly posterior to the short second dorsobronchus and travels through the middle of the anterior portion of the lung. Both rami show subdivisions along their peripheries and at the distal limits by lateroventral ramus anastomoses with a quaternary bronchus from the secondary ostium of the intermediate airsac during the eleventh day of incubation.

The first lateroventrobronchus appears to be the homolog of the first laterobronchus of Locy and Larsell (1916); however, the anterior ramus is similar in general destination to the main trunk of the first dorsobronchus.

The Second Lateroventrobronchus (second laterobronchus of Locy and Larsell, 1916).—This and the preceding bronchus originate on the lateral surface of the anterior vestibular region at the same level and at the same time. Near its base it gives rise during the eighth day of incubation to a laterally projecting tertiary bronchus which subdivides sending quaternary branches to the lateral and dorsolateral margins of the lung. The secondary bronchus bifurcates distally during the sixth day of incubation to give rise to a ventral and an anterolateroventral ramus. The distal portion of the latter ramus anastomoses with the most posterior quaternary bronchus from the secondary ostium of the intermediate airsac by eleven days incubation.

The Third Lateroventrobronchus (third laterobronchus of Locy and Larsell, 1916).—This bronchus arises at four days incubation on the lateroventral surface of the mesobronchus immediately distal to

the point where the embryonic vestibulum curves posteriorly and begins to decrease in diameter (Fig. 6). It projects toward the lateroventral margin of the lung where, at five days incubation, the distal end curves sharply laterally, posteriorly and dorsally, and increases slightly in diameter.

The gradual expansion of the third lateroventrobronchus outside the lung establishes the *anterior abdominal airsac*. This airsac at first has a broad connection to the lung because of its origin from the sub-apical rather than the apical end of the secondary bronchus.

The entire curved expanded portion of the secondary bronchus near the lung surface lies outside the lung by seven days incubation. By nine days the apical end of the secondary bronchus has given rise to numerous tertiary bronchi within the lung. The anterior abdominal airsac by this time has increased its size in the diaphragmatic tissue so that the airsac is connected to the lung by means of a primary ostium (proximal portion of the original secondary bronchus) and a secondary ostium (distal portion or apical end of the original secondary bronchus).

The Fourth Lateroventrobronchus (the fourth laterobronchus of Locy and Larsell, 1916).—This structure originates at about eighty-four hours incubation as a projection from the ventrolateral surface of the mesobronchus directly posterior to the orifice of the preceding lateroventrobronchus and, like the latter, reaches the lateroventral margin of the lung in the adult. The general contour of the fourth is like that of the third. The curved distal end, however, does not bulge out of the lung as an airsac. The region proximal to the curve does not expand in diameter. A tertiary bronchus, arising near the base of the secondary, courses laterally toward the lung border and runs a course parallel to that taken by its counterpart from the third lateroventrobronchus.

The Fifth Lateroventrobronchus (the fifth laterobronchus of Locy and Larsell, 1916).—The fifth bronchus originates at six days incubation as a lateroventral projection from the mesobronchus posterior to the origin of the fourth lateroventrobronchus and by the seventh day of incubation reaches the lung margin.

This secondary bronchus is curved apically in a manner similar to but less distinct than the curvature of the preceding secondary bronchus in this group. The laterally projecting tertiary bronchus near the base of the secondary bronchus originates during the seventh day of incubation and travels a course parallel to that of its counterpart from the preceding secondary bronchus in this group.

The Sixth Lateroventrobronchus (the sixth laterobronchus of Locy and Larsell, 1916).—This structure originates at the same time as and posterior to the orifice of the preceding secondary bronchus in this group. The general growth and destination of this secondary bronchus follows that given for the fifth lateroventrobronchus.

The Seventh, Eighth and Ninth Lateroventrobronchi.—These are

of doubtful homology to any secondary bronchus given by Locy and Larsell (1916).

The Seventh Lateroventrobronchus.—This secondary bronchus arises by six days of incubation as an anterolateroventral projection from the lateroventral surface of the mesobronchus immediately distal to the mesioventral curve in the posterior end of the mesobronchus. By nine days incubation it reaches its definitive position in the lung. The proximal portion of this secondary bronchus comes to lie in a plane parallel with that of the dorsal floor of the lung by the eleventh day of incubation. During the preceding day the mouth of this secondary bronchus becomes widened slightly and shifts its position from the mesobronchus to the airsac side of the ostium of the posterior abdominal airsac. That portion of the secondary bronchus which now lies outside the lung and makes a secondary connection between the lung and the airsac corresponds to a recurrent bronchus of previous authors.

The Eighth and Ninth Lateroventrobronchi.—These structures arise posterior to the seventh secondary bronchus in this group. The eighth lateroventrobronchus occurs anterior and dorsal to the ninth which lies on the lateroventral surface of the mesobronchus nearest the orifice of the posterior abdominal airsac. These two secondary bronchi have destinations similar to that given for the seventh lateroventrobronchus, and like it, their ostia become located on the airsac side of the ostium of the posterior abdominal airsac by the eleventh day of incubation.

DISCUSSION

The mesobronchus of the house sparrow shows much greater curvature immediately distal to the embryonic vestibular region than has been described for other species. The secondary bronchi in this species have been termed mesiobronchi, lateroventrobronchi, and dorsobronchi to give more accurate designation of their points of origin than is possible with earlier terminology. Huxley (1882) originated entobronchi to signify internal secondary bronchi. Locy and Larsell (1916) used entobronchi for the homologs of Huxley's entobronchi but used ectobronchi for the more anterior of the dorsally directed secondary bronchi from the vestibular and postvestibular region in the chick embryo. The use of the terms external and internal are likewise not sufficiently specific. Unlike Campana (1875) and Locy and Larsell (1916) no special consideration is deemed necessary for subdivisions of the secondary bronchi other than the use of the term *ramus* and the numerical treatment of successive tertiary bronchi from any given secondary bronchus. The consideration of certain tertiary bronchi as dorsobronchi by Locy and Larsell (1916) is not considered valid because such branches are not secondary bronchi but tertiary bronchi. The term secondary bronchus is restricted to a bronchus originating on the mesobronchus. This definition is in distinction to the minute air capillaries that are observed in later embryology. Table I compares the individual secondary bronchi of the house sparrow with the

TABLE I.—Comparison of terminology of secondary bronchi

House Sparrow (present paper)	Duck (Saphey, 1847)	Chicken (Campana, 1875)	Duck and Apteryx (Huxley, 1882)	Chicken (Locy and Larsell, 1916)
Mesio bronchus No. 1	Diaphragmatic No. 1	Divergent No. 1	Entobronchus No. 1	Entobronchus No. 1
Mesio bronchus No. 2	Diaphragmatic No. 2	Divergent No. 2	Entobronchus No. 2	Entobronchus No. 2
Mesio bronchus No. 3	Diaphragmatic No. 3	Divergent No. 3	Entobronchus No. 3	Entobronchus No. 3
Mesio bronchus No. 4	Diaphragmatic No. 4	Divergent No. 4	Entobronchus No. 4	Entobronchus No. 4
Mesio bronchus No. 5	Costal No. 6	Internal No. 5	Ectobronchus **	Ectobronchus No. 5
Dorsobronchus No. 1	Costal No. 1	Internal No. 1	Ectobronchus **	Ectobronchus No. 1
Dorsobronchus No. 2	Costal No. 2	Internal No. 2	Ectobronchus **	Ectobronchus No. 1
Dorsobronchus No. 3	Costal No. 3	Internal No. 3	Ectobronchus **	Ectobronchus No. 2
Dorsobronchus No. 4	Costal No. 4	Internal No. 4	Ectobronchus **	Ectobronchus No. 3
Dorsobronchus No. 5	Costal No. 5	Internal No. 6	Ectobronchus **	Ectobronchus No. 4
Dorsobronchus No. 6	Costal No. 7	Internal No. 7	Ectobronchus **	Ectobronchus No. 4
Dorsobronchus No. 7	Costal **	Internal **	Ectobronchus **	Ectobronchus No. 6
Dorsobronchus No. 8	*	*	*	***
Dorsobronchus No. 9	*	*	*	***
Lateroventrobronchus No. 1	*	*	*	Laterobronchus No. 1
Lateroventrobronchus No. 2	*	*	*	Laterobronchus No. 2
Lateroventrobronchus No. 3	Branch of Mesobronchus	External No. 1 External No. 2	Branch of Mesobronchus	Laterobronchus No. 3
Lateroventrobronchus No. 4	*	External No. 3	*	Laterobronchus No. 3
Lateroventrobronchus No. 5	*	External **	*	Laterobronchus No. 4
Lateroventrobronchus No. 6	*	External **	*	Laterobronchus No. 5
Lateroventrobronchus No. 7	*	*	*	Laterobronchus No. 6
Lateroventrobronchus No. 8	*	*	*	***
Lateroventrobronchus No. 9	*	*	*	***

* Bronchial group not described.

** Bronchial group described but homology not certain.

*** Homology of bronchial groups not determined.

probable homologs in other species as described by previous workers.

Special attention must be called to certain features of the house sparrow. The anterior four mesio bronchi are undoubtedly the homologs of the first four secondary bronchi described in other groups as arising distal to the entrance of the primary bronchus into the lung. The fifth mesio bronchus, though it arises from the posterior third of the mesobronchus, occupies the mesial, posterior area of the lung and thus fits into the group here termed mesio bronchi. On the basis of the actual secondary bronchi in the chicken as described by Locy and Larsell (1916), the number of true dorsobronchi from the posterior region of the mesobronchus in the chicken is greater than in the house sparrow. The number of entobronchi and mesio bronchi are the same except for the fifth mesio bronchus which corresponds to their fifth ectobronchus.

The number of dorsobronchi from the vestibular and immediate postvestibular region in the house sparrow is the same as the number of ectobronchi in the chicken except for the first and second dorsobronchi which are the apparent homologs of the branch and the main

TABLE II.—Time of origin of secondary bronchi

House Sparrow	Days of Incu- bation	Chicken (Locy and Larsell, 1916)	Days of Incu- bation
Mesio bronchus No. 1	3	Entobronchus No. 1	5¼
Mesio bronchus No. 2	3½	Entobronchus No. 2	5½
Mesio bronchus No. 3	3½	Entobronchus No. 3	5½
Mesio bronchus No. 4	3½	Entobronchus No. 4	6
Mesio bronchus No. 5	3¾	Ectobronchus No. 5	*
Dorsobronchus No. 1	3½	Branch of Ectobronchus No. 1	6
Dorsobronchus No. 2	3	Ectobronchus No. 1	6
Dorsobronchus No. 3	3½	Ectobronchus No. 2	6
Dorsobronchus No. 4	3½	Ectobronchus No. 3	*
Dorsobronchus No. 5	6	Ectobronchus No. 4	*
Dorsobronchus No. 6	6	Ectobronchus No. 6	**
Dorsobronchus No. 7	6	***	
Dorsobronchus No. 8	6	***	
Dorsobronchus No. 9	6	***	
Lateroventro bronchus No. 1	4	Laterobronchus No. 1	6
Lateroventro bronchus No. 2	4	Laterobronchus No. 2	6
Lateroventro bronchus No. 3	4	Laterobronchus No. 3	6
Lateroventro bronchus No. 4	4	Laterobronchus No. 4	**
Lateroventro bronchus No. 5	5½	Laterobronchus No. 5	**
Lateroventro bronchus No. 6	5½	Laterobronchus No. 6	**
Lateroventro bronchus No. 7	6	***	
Lateroventro bronchus No. 8	6	***	
Lateroventro bronchus No. 9	6	***	

* Exact time not stated; figures show structure by end of seventh day.

** Exact time not stated; figures show structure by end of eighth day.

*** Homology not determined.

stem of the first ectobronchus in the chicken. The last three dorso-bronchi in the house sparrow may correspond to recurrent bronchi of the posterior abdominal airsacs figured by Juillet (1912), Schulze (1912), Locy and Larsell (1916), or to the posterior dorsobronchi in the White Pekin duck described by Delphia (1958).

The first lateroventrobronchus in the house sparrow represents a possible intergrade between the lateroventrobronchi and the dorso-bronchi. The destination of its anterior ramus is in the most ventral, anterior region that is occupied by the anterior projection of the first dorsobronchus. The third lateroventrobronchus (origin of the anterior abdominal airsac) in the house sparrow is not only the homolog of the laterobronchus number three in the chicken (Locy and Larsell, 1916) but undoubtedly the homolog of the "branch" of the mesobronchus in *Apteryx* cited by Huxley (1882) for the origin of the equivalent of the anterior abdominal airsac. It has been observed (Delphia, 1958) that the third laterobronchus in the duck is the homolog of the third laterobronchus of the chicken (Locy and Larsell, 1916). The three posterior lateroventrobronchi in the house sparrow are possible homologs of the lateroventral groups of recurrent bronchi of the posterior abdominal airsac figured for numerous species by Juillet (1912) and Schulze (1912) and for the chicken by Locy and Larsell (1916), or they are the homologs of the posterior laterobronchi in the White Pekin duck (Delphia, 1958).

Locy and Larsell (1916) give the only complete description of the development of the secondary bronchi. Table II compares the time of origin of the secondary bronchi in the house sparrow (an altricial bird with a thirteen-day incubation period) with the apparent homologs in the chicken (a precocial bird with a twenty-one day incubation period).

The secondary bronchi in the house sparrow appear and develop earlier than in the chicken. This is in contrast to the redwing, *Agelaius phoeniceus* (Linnaeus) in which only eight secondary bronchi have been found by six days incubation (Daniel, 1957). The redwing and the house sparrow both have fewer secondary bronchi than the chicken.

SUMMARY

The time of origin, point of origin and general destination of each secondary bronchus is described for the house sparrow. Detailed description is given for the development of the mesobronchus, secondary bronchi and tertiary bronchi concerned with the origin of the individual airsacs. Primary and secondary ostia of the intermediate and anterior abdominal airsacs are described. Migration of origins or mouths of secondary or tertiary bronchi from the lung to the airsac side of an airsac ostium are given for certain airsacs.

The individual secondary bronchi are compared with those described in other species. The time of origin of the secondary bronchi in the house sparrow are compared with those of the chicken.

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Ecological Relationships Between Vegetation and the Distribution of Land Snails in Montana, Colorado and New Mexico

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ABSTRACT: Thirty-two species and subspecies of shelled land mollusks were collected. Ninety-nine per cent of the snails were associated with some form of deciduous tree, usually aspen. Food chain relationships between aspen and land snails appear likely. The amount of available calcium also is a factor noted to be related to vegetation and affecting snail distribution. Because of these relationships, it is proposed that snail distribution be reported in terms of associated vegetation rather than altitude. Snail distribution in burned areas is also discussed. Chance distribution appears unlikely to be the only method involved and small, permanent populations within conifers are suggested to occur. *Vertigo gouldi arizonensis*, *Gastrocopta pilsbryana* and *Striatula meridionalis* are reported as new records for the state of Colorado.

Land areas are often characterized by their dominant vegetation since the trees and plants which cover an area are easily seen and recognized by even a casual observer. This is particularly true in the mountainous regions of the western United States where the various plant formations are frequently composed almost exclusively of one or two tree species and where the boundary lines between major formations are often clearly defined as a result of physiographic and ecological factors. That the distribution of the plants may be expected to have a marked influence upon the distribution of land mollusks is self-evident although some discussion of the mechanisms involved is presented here. It is strongly suggested that future molluscan records be reported in terms of the vegetation of the collecting site instead of the altitude as is frequently done. Obviously the environment at 10,000 feet at Santa Fe, New Mexico, the southernmost point of the area investigated, differs markedly from that at the same altitude in Glacier National Park, Montana, the northernmost point of investigation. Opposing slopes on a single mountain are often covered by conspicuously different vegetation as a result of exposure to wind and snow, varying amounts of insolation and other ecological factors. To be meaningful, altitude records for snails must be adjusted since latitude and local conditions prevent direct comparisons, while reports including observations of vegetation are immediately comparable.

Correlations between 15 major plant associations and the occurrence of various species of land snails are discussed in this paper. Field work was carried on in Colorado and north-central New Mexico during the summer of 1958, supported by grant number 228-J of the

TABLE I.—The number of snails collected in each of 15 vegetation types

[illegible]

TABLE I.—(continued)

<i>Discus shimeki</i>	5	5	141	5	20	5	181
<i>cockerelli</i>	1						1
<i>Punctum minutissimum</i>	6		1				7
<i>Succinea avara</i>				2			2
<i>Succinea grosvenori</i>	4	2				2	10
<i>Pupillidae</i>			15				15
<i>Gastrocopta pilsbryana</i>							
<i>Gastrocopta pilsbryana</i>						1	1
<i>amissidans</i>	1						1
<i>Pupilla cf. hebes</i>	140	2	99	67		22	330
<i>Pupilla blandi</i>	7		16				24
<i>Pupilla muscorum</i>	10	10	5	7	1		33
<i>Vertigo concinnula</i>							
<i>Vertigo gouldi</i>			11			7	18
<i>arizonensis</i>							
<i>Vertigo gouldi</i>	2						2
<i>basidens</i>		7					7
<i>Vertigo ovata</i>							
<i>Vertigo modesta</i>	4			2	7	6	19
<i>parietalis</i>	2			1			3
<i>Columella edentula</i>	89		80	25		1	195
<i>Vallonia cyclophorella</i>		1					1
<i>Vallonia albula</i>	3			25		89	117
<i>Vallonia gracilicosta</i>	4		1	1			6
<i>Vallonia sp.</i>	137					3	140
<i>Zoogenetes harpa</i>	10	1	1	2		1	15
<i>Cionella lubrica</i>	3	3		1			7
Unknowns	714	0	492	289	33	158	1906
Total							

American Philosophical Society. Supplementary investigations in Montana during the summer of 1959 were supported by a grant from the Society of Sigma Xi.

Collecting stations were established in Mesa Verde, Glacier and Rocky Mountain National Parks. The writer wishes to thank the superintendents and staffs of those parks for their cooperation.

Most collections were made at scattered points in the mountainous portions of Montana, Colorado, and New Mexico. Seventy-two stations were sampled in the latter two states. These stations ranged in altitude from 5,500 to 12,300 feet and are the ones included in the data in Table I. Less extensive collections, made in Montana, are not included in the tabular material although the discussion does include such data.

Each station represented an area of less than 200 square yards in which an intensive search was made for mollusks. Collections were not made within a given period of time or over a specified area. The greatest amount of time was spent at those stations which were most productive. Such methods yielded the largest number of specimens for taxonomic study, a primary purpose of this investigation, but rendered impossible the application of some types of statistical analysis to the data.

ECOLOGICAL DISCUSSION

Fifteen distinct plant associations were recognized and are listed in Table I. The common names which are used following Harrington (1954). The presence of deciduous trees is closely linked to the distribution of western land mollusks. Forty-eight per cent of the snails were collected at 25 stations in deciduous plant associations. Virtually all of the other snails were collected at another 16 stations where deciduous trees represented a significant fraction of the dominant vegetation. Thus, 99 per cent of the entire number of snails collected were found at 44 stations, or only 57 per cent of the total number of stations. The single species of deciduous tree present at almost all of these stations was quaking aspen, *Populus tremuloides*. This association between aspen and snails may be related to the source of organic residues in the soil. Burch (1955) showed a correlation between the amount of organic matter which plants supplied to the soil and the distribution and abundance of snails in eastern forests, and a similar correlation is likely to exist in the west. It is also probable that aspen leaves or molds and fungi growing upon fallen aspen are directly associated with snails in a food chain relationship.

It is well known that the pH of soil is strongly influenced by the type of vegetation growing upon the soil. Conversely, pH may also limit the plants which can grow in a particular area. In general, coniferous forests are found upon acid soils. Deciduous forests may be found in alkaline areas but are not necessarily restricted to them. A small number of pH readings were made of the soil at various collecting sites. A difference of only 0.4 existed between the soil pH

beneath aspens where snails were present and the soil pH beneath lodgepole pine where no snails were found. Both stand of trees were growing on the same glacial moraine and were adjacent to each other. It is unlikely that the slight differences observed in the pH are responsible for the differences in the snail populations and it would be inaccurate to consider soil pH as a major factor in determining the distribution of snails, although this occasionally has been done. Of greater significance is the availability of calcium. Karlin (1956) has shown that numerous snails occurred in greenhouses where acid soils were found. In those soils, high levels of soluble calcium were produced by extensive fertilization. Joffe (1949) indicated that large quantities of calcium are returned to the soil by decomposing leaves and logs where it may form an insoluble Ca-humate upon drying. Snails which are able to utilize either soluble or insoluble calcium might survive in areas of acid soil. Records (Van Cleave, 1959) indicate that snails of several species are seasonally abundant in the acid duff of Mesa Verde National Park, where limestone outcroppings are unknown and where the dominant trees are conifers, pinon pine and juniper. It would appear that Oosting's statement (1950), "With such a variety of things that may be affected by soil acidity, it should be suspected that a simple relationship between pH and plant responses does not exist . . . pH alone cannot be the limiting factor," is justified for snails as well as plants.

An interesting problem is presented by the almost complete absence of snails from the coniferous forests which were studied. If snails are most frequently associated with aspen, a tree which follows fires in the pine, spruce, and fir forests of the region investigated, where do the snails originate? Heyward and Tissot (1936) have shown the ability of soil organisms to survive in burned-over areas, although their numbers are significantly reduced. The most likely speculation is that populations of snails, too small to be readily detected, are always present in coniferous areas. Careful sampling at 18 stations would indicate that such is not the case, however. A total of only seven snails was found at two stations in pine woodlands while not a single snail could be located in the spruce-fir forests. Isolated stands of aspen within large stands of spruce and fir invariably had snail faunas.

Possible distribution by birds and other animals apparently cannot account for all of the snail colonies which arise in new stands of aspen. Adventitious or accidental transport of snails into recently burned areas involves what Baker (1958) referred to as small number chance based solely upon luck. One snail species might even be expected to be distributed over a relatively small area within reasonable periods of time on such a chance basis, but this does not satisfactorily explain the presence of many species in almost all aspen woods.

Burned areas were visited in Glacier National Park, Montana, twenty-three years after the fire. Living snails were found associated with burned stumps of alpine fir and the Engelman spruce which

were being replaced by lodgepole pine and aspen. Burns only five and seven years old were also visited. No snails were found in those areas although replacement by lodgepole pine, aspen and larch was well initiated. An apparently recent burn of aspen, date of burning unknown, was found to contain a number of species and individuals of living snails. This latter observation suggests that snails can and do survive fires since it is likely that the aspen contained snails prior to burning. No conclusions can be drawn concerning the presence of snails in what formerly were coniferous woods. Despite the lack of evidence now available, it appears most logical to assume that very small snail populations do exist in most coniferous woods until fire-produced changes in the environment permit a rapid population increase.

MOLLUSCAN SPECIES COLLECTED

A total of 32 species and subspecies of land snails were collected. Slugs are not included in the list of species given in Table I, since they will be the subject of a separate paper. All scientific names in Table I follow Pilsbry (1939-1948).

Three of the species are new records for the state of Colorado. The ranges of many other species reported by Henderson (1907, 1924, 1936) and Pilsbry (1939-1948) have been extended.

Thanks are offered to Dr. Henry van der Schalie for assistance in identifying or checking some of the molluscan material. Examples of all the species collected have been deposited in the author's collection and/or that of the Museum of Zoology of the University of Michigan.

Some notes of particular interest follow:

A single individual of *Striatura meridionalis* was found in the Graham Creek campground on the east shore of Lake Vallecito near Durango, Colorado, thus representing a new record for the state. It was associated with several other species of snails in a mixed forest of lodgepole pine and quaking aspen.

Two individuals of *Succinea grosveneri* were collected in Mesa Verde National Park, Colorado. Both were found in sandy exposed situations in piñon pine and juniper forests. However, both snails were found within 6 feet of permanent streams, thus suggesting that the micro-habitats may not have been the extreme xeric ones indicated by Shimek (1935) for this species.

Fifteen individuals of *Gastrocopta pilsbryana* were collected at two stations on the east shore of Lake Vallecito near Durango, Colorado. These apparently represent the first records for this species in Colorado, although it is reportedly distributed abundantly in New Mexico not far to the south. There are also records from Utah to the west, thus suggesting that future finds may show a continuous distribution in suitable areas throughout southern Colorado. Both stations were characterized by a lodgepole pine-quaking aspen association. One typical individual of *Gastrocopta pilsbryana amissidens*

was collected together with *pilsbryana* proper. Since modern genetic concepts do not allow for synpatry, it is suggested that *amissidens* may not be a valid subspecies but only a variant.

Eighteen individuals of *Vertigo gouldi arizonensis* were collected on the east shore of Lake Vallecito near Durango, Colorado. This is still another new state record to come from that area. The previous distribution records for this species and others found with it at Lake Vallecito suggest that the fauna of the area has strong affinities to that of the mountains of New Mexico, 100 miles or more to the south.

Columella edentula was found in both northern and southern Colorado although only three individuals were collected, one at each of three localities. Pilsbry (1948) does not include Colorado in the known range of this northern species. However, he suggests that some of the Colorado records for *C. alticola* (Ingersoll) might actually refer to this species. Henderson (1924) does include two Colorado records for *C. edentula*. It is likely that this species occurs sporadically in the mountains much further south than previously suspected.

Zoogenetes harpa is a boreal species extending southward only at high elevations. Colorado localities near the 40th parallel represent the southernmost limit of its reported range (Pilsbry, 1948). Three individuals were found during this study at Lake Vallecito in southern Colorado, thus extending the known range of this species approximately 200 miles further south.

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Factors Influencing the Local Distribution of Shrews

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ABSTRACT: A field study was made of the factors influencing the local distribution of *Sorex cinereus* and *Blarina brevicauda* in southern Michigan. The environmental factors considered were vegetation type, cover (fallen trees, brush, leaf litter), temperature, food, moisture and interspecific competition. *Blarina brevicauda* was found only in moist situations but avoided standing water. It was scarce or absent in those habitats in which the available food supply (consisting of the larger forms of invertebrates) was low. Vegetation, type of cover, temperature, and interspecific competition were not important factors. *Sorex cinereus* occurred in all habitats except upland hardwoods. The reason for the avoidance of this habitat was not determined, but it apparently was not a response to the type of vegetation. *Sorex* was relatively less abundant in the drier situations than was *B. brevicauda* and did not avoid standing water. *S. cinereus* may be able to utilize smaller food items (collembolans, ants, spiders) than *B. brevicauda*, so that its local distribution is not influenced by the availability of the larger invertebrates. Type of cover, temperature, and interspecific competition were not important factors in its local distribution.

Shrews have been found to normally inhabit moist situations (Pruitt, 1953, 1959; Manville, 1949; Wetzel, 1958). Such a restriction to moist areas most likely results from a large turnover of water by shrews (Chew, 1951). Pruitt (*op. cit.*) has further analyzed the physical factors influencing the local distribution of shrews and found both temperature and moisture to be important factors. The relative importance of the various biotic factors (i.e., food availability, vegetation type, and interspecific competition) have not been thoroughly investigated. Pearson (1947) has shown that shrews have high metabolic rates and as a result require large intakes of food. As a result one might expect the availability of food to play an important role in the local distribution of shrews.

The present paper contains data pertaining to the masked shrew, *Sorex cinereus*, and the shorttailed shrew, *Blarina brevicauda*, obtained during a study of the factors influencing the local distribution of small mammals in southern Michigan. Data concerning other species will be presented elsewhere (*Microtus pennsylvanicus* and *Synaptomys cooperi*, in press; *Peromyscus leucopus* and *Zapus hudsonius*, in preparation). Most of the habitats studied had conditions moist enough to be considered favorable in regard to this factor. Shrews did not occur in all study areas, however; it was desired, therefore, to determine the factors influencing distribution within these moist areas.

Acknowledgments.—The material presented here represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan. I am grateful to Drs.

W. H. Burt, W. S. Benninghoff, F. C. Evans, and H. van der Schalie for their assistance and encouragement during the course of the study. I wish also to thank my wife, Mary Ruth, for doing many of the compilations. The field work was done under the auspices of a Horace H. Rackham predoctoral fellowship.

DESCRIPTION OF THE STUDY AREA

All work was done on the University of Michigan's Mud Lake Research Area, located in northern Washtenaw County, Michigan. The study consisted essentially of three parts: (1) a generalized study of seven habitats (old field, marsh, bog mat, hardwood swamp, oak-hickory upland, spruce swamp, and spruce burn); (2) a more intensive study of the old field and marsh; and (3) studies along a series of transects. A description of the seven habitats and transects is given below (plant nomenclature follows that of Fernald, 1950). Complete vegetative descriptions and phytosociological tables are not given for the marsh, old field, and bog mat; these are published elsewhere (Getz, 1959).

Old Field.—A field abandoned for approximately 15 years. The vegetation consists primarily of *Poa compressa*, *Potentilla intermedia*,

TABLE I.—Partial Braun-Blanquet relevés from the swamp hardwoods. A, from the wet portion; B, from the moist portion. The numbers indicate abundance-cover and sociability estimates in that order (for scales see Dansereau, 1957).

Species	Relevé A	Relevé B
Tree stratum		
<i>Acer rubrum</i>	3.1	4.1
<i>Ulmus americana</i>	3.1	+1.1
<i>Betula lutea</i>	+1.1	2.1
<i>Populus tremuloides</i>		1.1
Shrub stratum		
<i>Rhamnus alnifolia</i>	2.2	1.1
<i>Rhus vernix</i>	2.3	
<i>Acer rubrum</i>	+1.1	+1.1
<i>Prunus</i> cf. <i>nigra</i>	+1.1	+1.1
<i>Vaccinium corymbosum</i>	+2	+1.1
Field stratum		
<i>Osmunda cinnamomea</i>	3.3	2.3
<i>O. regalis</i>	+2	+2
<i>Onoclea sensibilis</i>	2.2	1.2
<i>Symplocarpus foetidus</i>	3.2	1.2
<i>Maianthemum canadense</i>	1.3	2.2
<i>Coptis groenlandica</i>	+2	1.3
<i>Acer rubrum</i>	+1.1	2.1
<i>Parthenocissus quinquefolia</i>	+1.1	1.1
<i>Dryopteris spinulosa</i>	+2	+2

and *Daucus Carota*. The surface is partly covered by a moss, *Brachythecium* sp. The soil is primarily a sandy loam except in the low moist places which have a slightly higher humus content. In comparison with the other areas, the old field is dry.

Hardwood Swamp.—This habitat, characterized by a mature stand of hardwood trees (*Acer rubrum*, *Ulmus americana*, and *Betula lutea*), lies in a low wet area. Although the soil is moist throughout the year, the northeastern (slightly higher) portion is somewhat drier. The lower portion is almost completely inundated during the fall and spring, and during the winter months when not frozen. The higher region contains a few small pools of standing water during these times.

A shrub stratum of young trees, *Rhus vernix* and *Ilex verticillata*, is present in the wetter places. A field stratum which consists of *Osmunda cinnamomea*, *O. regalis*, *Dryopteris spinulosa*, *Onoclea sensibilis*, *Symplocarpus foetidus*, *Impatiens capensis*, *Rubus pubescens*, *Coptis groenlandica*, and *Maianthemum canadense* is also well developed here. Shrub and field strata are little developed in the drier region (Table I).

TABLE II.—Partial Braun-Blanquet relevés from the spruce — birch — larch swamp and the spruce burn. The numbers indicate abundance-cover and sociability estimates in that order (for scales see Dansereau, 1957).

Species	Spruce area	Birch- larch area	Burn area
Tree stratum			
<i>Picea mariana</i>	4.1	-----	-----
<i>Larix laricina</i>	1.1	2.1	-----
<i>Betula lutea</i>	-----	4.1	-----
Shrub stratum			
<i>Vaccinium corymbosum</i>	2.2	2.2	1.3
<i>Gaylussacia baccata</i>	+ .2	2.2	-----
<i>Ilex verticillata</i>	+ .1	-----	-----
<i>Larix laricina</i>	-----	+ .1	1.1
<i>Picea mariana</i>	-----	+ .1	2.1
<i>Acer rubrum</i>	-----	1.1	-----
Field stratum			
<i>Maianthemum canadense</i>	+ .1	2.2	-----
<i>Symplocarpus foetidus</i>	+ .2	-----	-----
<i>Sarracenia purpurea</i>	+ .2	-----	1.1
<i>Carex disperma</i>	+ .3	-----	-----
<i>Vaccinium corymbosum</i>	-----	1.1	-----
<i>Acer rubrum</i>	-----	1.1	-----
<i>Osmunda cinnamomea</i>	-----	+ .3	-----
<i>Dryopteris spinulosa</i>	-----	+ .2	-----
<i>Chamaedaphne calyculata</i>	-----	-----	4.5
<i>Vaccinium macrocarpon</i>	-----	-----	2.1

The relatively level surface of the drier portion is covered with a thin layer of leaf mold. The wet region is characterized by an irregular surface with hummocks (built largely by growth of *Osmunda cinnamomea*) rising approximately .25 meters above the surface. The hummocks are not covered by water during the wet season. *Sphagnum* sp. and other mosses are common here but are much less abundant in the drier sites. The wet portion is also characterized by having much more debris (deadfall timber and brush) on the surface.

The upper soil layers of this habitat are composed mainly of humus with only a small amount of mineral matter. A fibrous mass of roots gives the soil a spongy character.

Bog Mat.—A typical *Sphagnum* bog mat, located on the northern side of Mud Lake. The water level is usually 10 to 15 centimeters below the surface (in some places where the *Sphagnum* is absent, it is at the surface). The very wet substrate is composed almost entirely of peat with very little mineral matter. There are four distinct plant communities on the bog mat: (1) *Typha-Chamaedaphne*; (2) *Chamaedaphne*; (3) *Larix-Rhus*; and (4) *Carex-Scirpus*.

Black Spruce-yellow Birch-larch Swamp.—The vegetation of this habitat consists of two distinct types; a *Betula-Larix* swamp which gradates into a *Picea mariana* swamp (Table II).

The *Betula-Larix* portion is characterized by an open stand of *Betula lutea* and *Larix laricina*. A dense shrub stratum of *Vaccinium corymbosum*, *B. lutea*, and *Acer rubrum* is present. There are many fallen trees. The surface is covered with a leaf mold consisting mainly of birch leaves and larch needles. On lower ground some *Sphagnum* occurs.

The *Picea mariana* swamp contains sparse shrub and field strata. The canopy occurs to within 1 to 3 meters of the ground. The bases of the trees are surrounded by small, low hummocks rising 15 to 20 centimeters above the surface. These hummocks are covered by a litter layer of spruce needles and are comparatively dry. The low depressions contain *Sphagnum* and are moist. They hold standing water during the wet seasons.

The ground surface of the spruce stand presents the typical physiognomy of spruce growing on a shallow soil. Frost heaving and wind action have combined to produce either complete or partial windthrows. Owing to their shallow, spreading root system, the trees have raised portions of the soil surface, leaving open cavities below that are usually filled with water.

Spruce Burn.—A site within the spruce stand that burned approximately 27 years ago. It is characterized by a cover of *Sphagnum* with a uniform stand of leather-leaf (*Chamaedaphne calyculata*) and a few scattered small black spruce trees (*Picea mariana*). The surface is irregular with hummocks of *Sphagnum* up to half a meter in height surrounding the bases of the leather-leaf clones. Below the *Sphagnum* is a humus substrate containing some mineral matter and

charcoal, a remnant of the forest fire. The water table is .25 to .50 meters below the surface (depending upon the season). While the *Sphagnum* is relatively moist throughout the year, it is not so moist as that occurring in the bog. The hummocks in particular are relatively dry.

Oak-hickory Upland.—This habitat is located on an elevated glacio-fluvial deposit lying in a low marshy area. Its highest point is 4 to 5 meters above the surrounding marsh. It is covered by a mature oak-hickory stand. The dominant trees are *Carya ovata*, *Quercus alba*, and *Q. rubra*. A shrub stratum of young individuals of the dominant species, as well as *Pyrus coronaria*, *Prunus serotina*, and *Corylus americana* is of sporadic occurrence. Field stratum plants are common. The more abundant species are *Carex rosea*, *Aster macrophyllus*, *Galium boreale*, *Geranium maculatum*, *Pteridium aquilinum* var. *latiusculum*, *Rosa virginiana*, *Quercus alba*, and *Anemone thalictroides* (Table III). A leaf mold is well developed over most of the site although it is partially obscured by sedges (*C. rosea*) in the localities free of shrubs. Numerous fallen trees and decaying stumps occur throughout. The soil is dry in comparison with that of the hardwood swamp.

The physiognomy of the vegetation closely resembles the drier portion of the hardwood swamp. There is considerable difference, how-

TABLE III.—Partial Braun-Blanquet relevés from the oak-hickory. A, from a portion with underbrush; B, from a portion with little underbrush. The numbers indicate abundance cover and sociability estimates in that order (for scales see Dansereau, 1957).

Species	Relevé A	Relevé B
Tree stratum		
<i>Carya ovata</i>	4.1	1.1
<i>Quercus rubra</i>	4.1	
<i>Q. alba</i>	2.1	5.1
Shrub stratum		
<i>Corylus americana</i>	2.3	
<i>Prunus serotina</i>	2.1	+ .1
Field stratum		
<i>Carex cf. rosea</i>	2.2	4.3
<i>Aster macrophyllus</i>	3.3	2.3
<i>Galium boreale</i>	2.3	2.3
<i>Geranium maculatum</i>	2.1	2.1
<i>Pteridium aquilinum</i>	2.2	
<i>Rosa virginiana</i>	2.2	+ .1
<i>Corylus americana</i>	2.1	
<i>Quercus alba</i>	2.1	
<i>Anemone thalictroides</i>	1.1	1.1

ever, between that of the oak-hickory stand and wetter sites of the hardwood swamp.

Marsh.—The dominant plants in this habitat are sedges and grasses; one area contains primarily *Potentilla fruticosa* and another, a stand of *Solidago* sp. and *Aster* sp. There is considerable variation in species composition within the grass-sedge portion.

In general, the surface is low with the water table only a few centimeters below the surface. During the wet season, water stands over most of the area. Only the portions that support the *Solidago*, *Aster*, and *P. fruticosa* stands were not inundated during the study. Of these the *P. fruticosa* stand grows on the higher ground (.25 to 1.0 meter above the general level of the marsh surface). The soil throughout is typical of marshes (Dansereau, 1957); it contains much fibrous, peaty humus and a moderate amount of mineral matter. As indicated above, the soil moisture is high even when not inundated, being nearly saturated during the driest months. The sedges and grasses grow from small hummocks 5 to 10 centimeters in diameter and height. The spaces between the hummocks are usually free of living vegetation. In the slightly drier portions these hummocks may not be completely submerged during the wet season.

During the winter the dead vegetation falls over and forms a low canopy. Decaying vegetation also falls in between the hummocks to form a tangled mat that covers the surface. In the summer the grasses and sedges completely cover the surface.

Descriptions of the Transects.—Six transects were established to cross as many different habitats as possible. These transects were subdivided into different "segments" according to physiognomy of the vegetation, type of and moisture content of the substrate, leaf litter, and debris (logs, dead brush, and litter). A brief description of each of the 15 segments so established follows:

1. Moist, open swamp hardwoods.—Tree stratum well-developed (*Prunus virginiana*, *Betula lutea*, *Quercus macrocarpa*, and *Populus tremuloides*), canopy open; shrub stratum dense (*Rhus vernix*, *Vitis* sp., *Ilex verticillata*, *Acer rubrum*, and *P. tremuloides*); field stratum dense (*Impatiens capensis*, *Rubus pubescens*, *Vitis* sp., *Thalictrum dasycarpum*, *Aralia nudicaulis*, and *Onoclea sensibilis*); few mosses present; substrate primarily organic with some mineral matter present; moist; leaf mold thick; much debris on the surface (43% coverage). Length, 93 meters.
2. Wet, closed, swamp hardwoods.—Dense tree stratum (*Betula lutea*, *Acer rubrum*, and *Ulmus americana*), canopy closed; shrub stratum dense (*Rhus vernix*, *Ilex verticillata*, *A. rubrum*, and *B. lutea*); field stratum dense (*Osmunda cinnamomea*, *Onoclea sensibilis*, *Symplocarpus foetidus*, *Maianthemum canadense*, and *Rubus pubescens*); surface open between the clones of ferns; mosses abundant; substrate primarily organic with some mineral matter present, spongy; wet; leaf mold thin; much debris on the surface (28% coverage). Length, 312 meters.
3. Moist, closed, swamp hardwoods.—Tree stratum dense (*Acer rubrum* and *Ulmus americana*), canopy closed; sparse shrub and field strata;

- few mosses present; substrate primarily organic with some mineral matter present; moist; leaf mold thick; little debris on the surface (16% coverage). Length 156 meters.
4. Sedge-fern bog.—Tree stratum absent; shrub stratum sparse (*Rhus vernix* and *Larix laricina*); field stratum dense (*Typha latifolia*, *Scirpus acutus*, *Carex lasiocarpa*, and *Dryopteris Thelypteris*); substrate peat, covered with *Sphagnum*, little mineral matter present; wet; little debris on the surface (less than 1% coverage). Length, 120 meters.
 5. Larch bog.—Low tree stratum present (*Larix laricina*), canopy closed; shrub stratum dense (*L. laricina*, *Betula lutea*, *Rhus vernix*, and *Cornus stolonifera*); field stratum present (*Osmunda cinnamomea*, *O. regalis*, and *Dryopteris Thelypteris*); substrate peat, covered with *Sphagnum*, some mineral matter present; wet; some debris on the surface (less than 1% coverage). Length, 42 meters.
 6. Leather-leaf bog.—Tree stratum absent; very low shrub stratum present (*Chamaedaphne calyculata* and *Vaccinium macrocarpon*); sparse field stratum; substrate peat, covered with *Sphagnum*, little mineral matter present; wet; no debris present. Length, 132 meters.
 7. Cattail-leather-leaf bog.—Tree stratum absent; low shrub stratum present (*Chamaedaphne calyculata* and *Salix* sp.); field stratum dense (*Typha latifolia* and *Dryopteris Thelypteris*); substrate peat, covered with *Sphagnum*, some mineral matter present; very wet; some debris on the surface (less than 1% coverage). Length, 54 meters.
 8. Birch-larch swamp.—Tree stratum well-developed (*Larix laricina* and *Betula lutea*), canopy open; shrub stratum dense (*Vaccinium corymbosum*, *Acer rubrum*, *B. lutea*, and *Gaylussacia baccata*); field stratum present (*A. rubrum* and *Maianthemum canadense*); some mosses present; substrate *Sphagnum* and decaying organic material, some mineral matter present; moist; leaf mold on dry places; much debris on the surface (50% coverage). Length, 96 meters.
 9. Larch-spruce swamp.—Tree stratum very dense (*Larix laricina* and *Picea mariana*), canopy closed; shrub and field strata sparse; substrate organic with mineral matter present around the bases of the trees; wet; leaf mold thin; little debris on the surface (11% coverage). Length, 48 meters.
 10. Spruce burn.—Tree stratum absent; shrub stratum dense (*Picea mariana*, *Chamaedaphne calyculata*, and *Vaccinium corymbosum*); field stratum sparse; substrate organic with little mineral matter present and covered with *Sphagnum*; moist; no leaf mold present; little debris on surface (2% coverage). Length, 108 meters.
 11. Birch-poplar-maple swamp.—A few scattered trees (*Populus tremuloides*, *Acer rubrum*, and *Betula lutea*); shrub stratum dense (same species as tree stratum); field stratum present (*Maianthemum canadense*, *Onoclea sensibilis*, and sedges); some mosses present; much debris on the surface (38% coverage). Length, 120 meters.
 12. Oak-hickory upland.—Tree stratum dense (*Quercus alba*, *Q. rubra*, and *Carya ovata*), canopy closed; shrub stratum present (*Prunus serotina*, *Pyrus coronaria*, *Corylus americana*, and *Cornus racemosa*); field stratum present (*Galium boreale*, *Aster macrophyllus*, *Carex rosea*, and *Anemonella thalictroides*); substrate mainly mineral matter, some organic material present; dry; leaf mold well developed; little debris on the surface (15% coverage). Length, 144 meters.
 13. Composite marsh.—Tree and shrub strata absent; field stratum dense; forbs abundant (*Solidago* sp., *Aster* sp., and *Eupatorium purpureum*).

- some grasses and sedges present; substrate decaying organic material, some mineral matter present; wet; much debris on the surface (100% coverage). Length, 96 meters.
14. Grass-sedge marsh.—Tree and shrub strata absent; field stratum dense, primarily of grasses and sedges; substrate organic with some mineral matter present; wet; much debris on the surface (100% coverage). Length, 72 meters.
15. *Potentilla* marsh.—Tree and shrub strata absent; field stratum present, primarily *Potentilla fruticosa*, some grasses and sedges present; substrate organic, some mineral matter present; moist; much debris on surface (100% coverage). Length, 87 meters.

METHODS

Most of the methods have been described elsewhere (Getz, 1959 and in press). Only those methods pertaining directly to the shrews are given in detail here; the remainder are summarized. The period of the study was September, 1957, through September, 1958.

Generalized Study.—A rectangular study area was established in each of the seven habitats described above. Each study area, except that in the burn area, contained 75 trap stations placed in a grid pattern with a 12 meter interval. The burn area was small and contained only 30 stations. All areas except the old field and marsh were snap-trapped for two, three-night periods (one trap at each station). The live-trapping data (see below) were utilized to get comparable data from the marsh and old field. The areas were trapped once in the fall (October and November, 1957) and again in the winter (January, 1958).

Study of the Marsh and Old Field.—The entire old field (2.5 hectares) and a 4.4-hectare portion of the marsh were marked off in a grid pattern with a 12-meter interval. Both areas were live-trapped for five nights each month from September, 1957, through September, 1958. Because of the large number of stations in the marsh, two trapping periods were required to cover all the stations. Live-traps of the type described by Burt (1940) were utilized. The traps were checked twice a day, once at 0800 to 1100 and again from 1600 to 1800 (for dates of trapping see Getz, 1959).

The live-traps were not efficient in capturing shrews. Most were able to escape by raising the trap-door. As a result relatively few captures were recorded (243 individuals caught a total of 405 times during the entire study). From the odor and feces in the trap, it could normally be determined when a shrew had entered a trap. Most of the data concerning the distribution of shrews were, therefore, obtained from signs rather than from actual captures.

Trap mortality was high for those individuals captured. Twenty-two per cent of the first captures of *B. brevicauda* were dead in the traps while 26 per cent of those alive at the first capture eventually were found dead in the traps. Of 74 individuals of *S. cinereus* taken, only nine were alive when first captured and two of these were eventually found dead in the traps. The *B. brevicauda* population was

undoubtedly reduced somewhat and almost the entire *S. cinereus* population was apparently removed for none was captured after April.

Transect Studies.—A trapping station was located every three meters along each transect. Each station was trapped (one snap-trap per station) for seven nights during the first two weeks of September, 1958. The capture data for each of the 15 segments were converted to a common factor (number of captures per 500 trap nights) for comparisons.

STUDIES OF ENVIRONMENTAL FACTORS

The techniques employed in the study of the environmental factors have been given in detail elsewhere (Getz, 1959). The factors studied included vegetation (type and physiognomy), cover, moisture (including standing water), temperature, and food.

Vegetation.—Line intercept transects were studied to determine vegetation types in all seven areas as well as along the trapping transects. Phytosociological studies were also made in all seven habitats. These data have been used to determine the types of vegetation present as well as the physiognomy.

Cover.—The amount of cover (percentage of coverage) in the form of logs, stumps, brush, leaf mold, and other debris, was determined from the line intercept data.

Moisture.—Substrate moistures were determined by gravimetric methods. Samples were taken from each habitat several times during the course of the study. These showed that all areas except the old field have practically saturated substrates at all times. The depth of standing water at each station in the marsh was recorded during each trapping period. The standing water in the swamps and bog were also indicated on the line intercept transects.

Temperature.—Temperatures were determined by stations located in each habitat. A station consisted of three max-min thermometers measuring temperatures one meter above the surface, 2.5 centimeters above the surface (leaf litter or snow when it was present), and 4.0 centimeters below the surface. Thermometers recording surface temperatures were placed at different sites within the marsh, old field, and hardwood swamp to obtain comparisons.

Food.—Information concerning the food habits of shrews is given by Hamilton (1930, 1941), Eadie (1944), Ingram (1942), and Shull (1907). From the food items listed in these papers, as well as from my own observations on captive specimens, it appears that a shrew will eat almost any small invertebrate it encounters. Since no evidence is at hand to contradict this, I have assumed all terrestrial invertebrates available to shrews to be potential sources of food. By comparing the amount of food items in the various habitats a rough estimate can be obtained of the relative availability of food.

To obtain estimates of the amount of potential shrew food available, several methods of sampling were employed. The basic method of sampling in all areas was one similar to that described by Shelford

(1929). An open-topped, one-twelfth square meter sampling ring was utilized. Representative portions of each study area were chosen and the ring tossed into the sites with the sample being taken where the ring came to rest. All the invertebrates on the surface or in the upper five centimeters of the substrate were recorded. Six such samples were taken at each site studied.

In the areas in which they occurred, logs were turned and a count made of all invertebrates found under them. Measurements were then made of the area covered by each log, and the number of logs in the habitat was estimated. In those areas being live-trapped the number of invertebrates that congregated in and under the traps was noted. Pitcher plants were also examined, and the numbers of invertebrates in them recorded. Finally, general observations were made to further add to these data.

In determining the comparative amounts of food available in the various areas, the data from the ring samples were used as a base. The data obtained from the other sampling methods were then evaluated to give a better indication for each habitat. The individual animals were not weighed, but each individual was assigned a "mass number" based on its size (indications of relative sizes of the individuals were recorded in the original notations). These were then totaled to give a comparative figure for each habitat.

Admittedly, these results are subjective. Numerous sources of error are present, one of which is the possible rejection of certain species by the shrews. Other factors such as seasonal and daily variations in activity patterns would tend to influence the apparent availability of food at any given time. The above sampling was done during May, 1958. Observations in all the habitats during the other months indicated that the relationships obtained in this study were not altered greatly.

STATISTICAL ANALYSIS

Those data that lend themselves to statistical treatment have been analyzed by use of the Chi-square test and the Spearman rank correlation coefficient (Siegel, 1956). In the following discussions the correlation coefficient (r_s) as well as the probability or level of significance (P), from Siegel (*op. cit.*), are given with statements of correlation or no correlation.

RESULTS

Blarina brevicauda

The shorttailed shrew is "most common in heavy forests and low, damp, swampy areas, but may be expected in practically every land habitat" (Burt, 1948). Other workers (Townsend, 1935; Pruitt, 1953; Enders, 1930; Dice and Sherman, 1922; Allen, 1938; and Wetzel, 1958) have demonstrated that *B. brevicauda*, occurs in most types of vegetation.

These same authors have also stated that *B. brevicauda* occurs in moist areas. Enders (*op. cit.*) further stated that it was more abun-

dant in well-drained (although moist) areas. Chew (1951) found that *B. brevicauda* had a high evaporation rate (twice that of *Peromyscus leucopus*). Furthermore it was unable to regulate evaporation in low humidities. This high evaporative loss indicates the necessity of a high humidity or a relatively high intake of free water to avoid desiccation. Pruitt (1959) found that *B. brevicauda* inhabited only those areas in which the soil moisture was high enough to saturate the air of its burrows. He concluded that a saturated air was required in the burrows of these animals in order for them to maintain a water balance. The food of *B. brevicauda* is composed of from 60 to 95 per cent water (Chew, *op. cit.*) This augments intake of free water.

Indications of a restriction to areas that have a well-developed leaf mold (Hanson, 1946; Pruitt, 1953) probably result from the indirect relationship of increased humidity under such a cover. In support of this, Jameson (1949) found that a leaf mold was not essential for the presence of *B. brevicauda*. Manville (1949) stated that "moisture seems to have somewhat less influence on the distribution of this species than on that of . . . *Sorex*."

Pearson (1947) found that *B. brevicauda* has a high metabolic rate (next to *S. cinereus* which had the highest rate of the 13 species tested). This indicates a need for an abundant supply of food. Hamilton (1930) has given data concerning the amount of food eaten by captive *B. brevicauda* that tend to confirm the voraciousness of this species. Eadie (1944) has shown *B. brevicauda* to feed extensively on *Microtus pennsylvanicus*; this relationship may influence its distribution.

Pruitt (1953, 1959) found that *B. brevicauda* avoids areas that display extreme temperature variations. However, I know of no studies concerning the temperature toleration of this mammal.

In the present study I attempted to investigate the influences of standing water, available food, and temperature upon this shrew. Information pertaining to vegetation, interspecific competition, and cover were also obtained. These are summarized under the appropriate headings.

Vegetation.—No response to the type of vegetation was indicated since *B. brevicauda* was present in most types ranging from grass-like to forested (Figs. 1 and 2). The high population densities in the

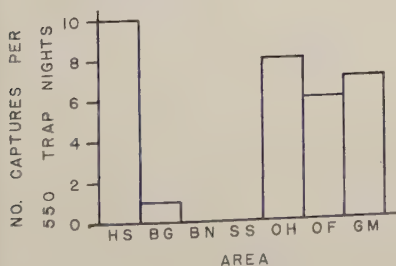


Fig. 1. — Relative abundance of *Blarina brevicauda* in the seven habitats of the generalized study. Fall and winter trapping data combined. HS, hardwood swamp; BG, bog mat; BN, burn; SS, spruce-birch-larch swamp; OH, oak-hickory; OF, old field; GM, grass-sedge marsh.

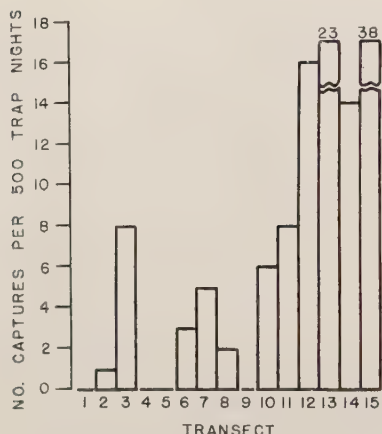


Fig. 2.—Transect captures of *Blarina brevicauda*

P. fruticosa area of the marsh (Fig. 3) appear to be a response to moisture conditions and not to the woody vegetation present in this area. Likewise, their absence in certain other types can be attributed to different factors as discussed below.

Cover.—The transect data showed that no correlation existed between the amount of cover (in the form of logs, brush, debris, etc.) in the various wooded habitats and the captures of *B. brevicauda* (r_s — .11; P , .05 = .714). This species was also abundant in habitats in which such cover was absent. Cover (as defined above), therefore, has no significant influence upon the local distribution of

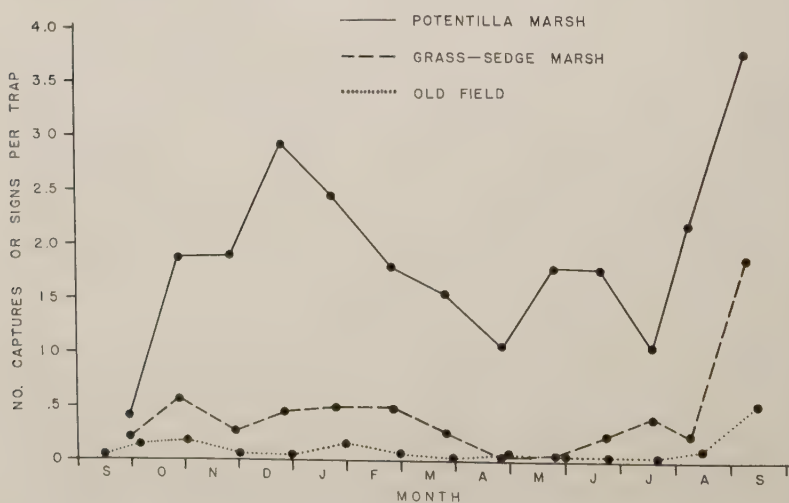


Fig. 3.—Captures and/or signs of *Blarina brevicauda* in the marsh and old field, September, 1957, through September, 1958

B. brevicauda. This appears particularly true in the birch-larch segment (No. 8) of the transects. This segment had a considerable amount of debris and logs on the surface and the soil was moist, but *B. brevicauda* was absent. Available food was low and appeared to be the limiting factor. Likewise, much cover was present in the hardwood swamp transect segments Nos. 1 and 2, but *B. brevicauda* was absent or quite scarce. No difference in number of captures occurred between segment No. 3 of the hardwood swamp, which had very little cover, and No. 11 of the birch-poplar-maple swamp, which had a great deal of cover. Leaf mold was not an important factor as *B. brevicauda* was abundant both where leaf mold was present and where it was absent (i.e., oak-hickory and marsh).

Moisture.—Avoidance of extremely dry areas was apparent from the live-trapping data of the old field (Fig. 3). Furthermore, most of the captures and signs were from the low, moist sites in the field.

Standing water was also avoided. Data from the marsh show very few captures or signs from stations that were inundated (Table IV). Furthermore, most of the inundated stations recording captures or signs were close to places where the surface was not covered with water. As soon as the standing water disappeared in the summer, *B. brevicauda* started moving into the portions formerly avoided. By September, 1958, the shorttailed shrew was distributed throughout most of the marsh.

The transect in the wetter portion of the hardwood swamp yielded few captures of *B. brevicauda*. Likewise no captures during the generalized study were obtained from the wetter portion of the study area. Water was present in this region during the fall, winter, and spring. Although it disappeared later in the summer, movement of *B. brevicauda* into the region may not have been rapid enough for the region to yield large numbers of captures. The fewer numbers on

TABLE IV.—Relation of captures and signs of *Blarina brevicauda* to depth of water. (Data represent compilations for all months standing water was present in the marsh.)

Average water depth ¹	No. of traps	No. of captures and signs	Average per trap
0	559	624	1.12
2.5	217	62	.28
5.0	100	5	.05
7.5	38	1	.03
10.0	63	2	.03
12.5	28	1	.04
15.0+	51	1	.02

¹ Depth of water measured in centimeters.

the bog may in part have resulted from excessive moisture, but food availability is probably a more important factor.

Food.—Since *B. brevicauda* is a rather large shrew, it tends to feed upon the larger species of invertebrates. The smaller food items (collembolans, ants, etc.) may be too small to furnish an adequate supply of food for *B. brevicauda*. This is in contrast to *S. cinereus*, which, owing to its small size, probably is more capable of capturing the smaller food items.

No correlation existed between the relative abundance of food in the various areas and the distribution of *B. brevicauda* (r_s , .15; P , .05 = .564). Similarly, no area had high population densities of *B. brevicauda* solely because of a greater availability of food (Fig. 4). This was particularly obvious in the higher parts of the old field during the summer. During this time, food availability was very high owing to the presence of numerous crickets, grasshoppers, and other insects. *B. brevicauda* almost completely avoided the area, however. A similar situation existed in the marsh. In the portion that contained standing water, food was more abundant than in the drier parts (e.g., *P. fruticosa* area). *B. brevicauda* avoided the former, however. Similarly, food was much less abundant in the drier parts of the hardwood swamp than in the wetter places, but *B. brevicauda* was much more abundant in the former.

Low amounts of available food appeared to have a definite influence on the local distribution of *B. brevicauda*. The burn and spruce-birch-larch swamp appeared to have favorable amounts of moisture and cover, but were deficient in available food. *B. brevicauda* was almost entirely absent from these two areas. Most of the individuals that were captured in the burn area were from near the edge of a birch-poplar stand that had a greater supply of food. The low food availability on the bog mat is probably the main factor responsible for the low numbers of *B. brevicauda* in this area.

Temperature.—Except in areas with little vegetation (i.e., the

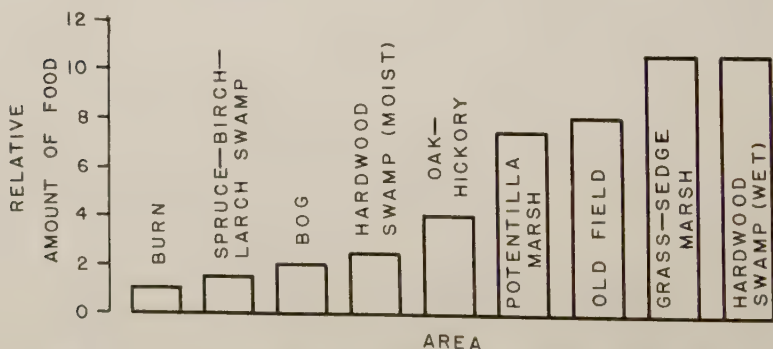


Fig. 4.—Relative abundance of available food (larger invertebrates) for shrews. Based on the burn area as one

parts of the old field in which the growth of grass was sparse) temperature probably did not exert a significant influence upon the local distribution of *B. brevicauda*. In some areas the stratum occupied by the shrews had extremely low temperatures. One such area was the hardwood swamp (Fig. 5); this area was inhabited by *B. brevicauda* during the winter. Observations of tracks and signs made during one of the coldest nights of the year, 4 January 1958 (surface temperature low of -20°C), showed that *B. brevicauda* had been active in all areas in which this species occurred. In most areas studied a sufficient amount of vegetation occurred for the animals to obtain shelter during periods of extremely low temperatures should they desire to do so. Areas such as the marsh (grass-sedge type), bog mat, and burn had relatively moderate temperatures (Getz, in press), but were not utilized extensively by *B. brevicauda*.

Few captures were obtained in the higher parts of the old field during the winter. As vegetation was sparse here and no other cover

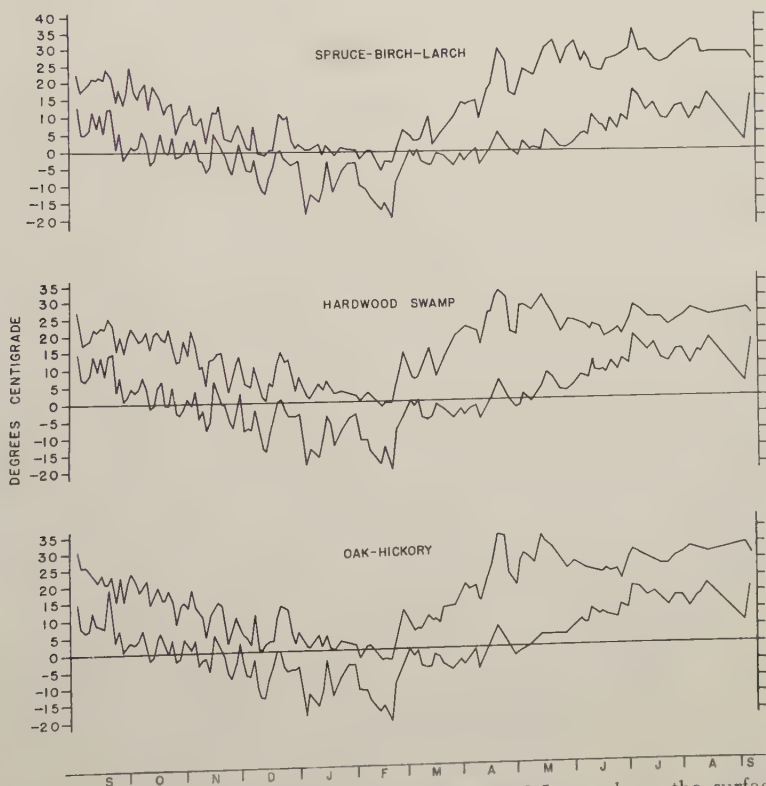


Fig. 5.—Maximum and minimum temperatures 2.5 cm above the surface. Thermometers were checked every two to four days, September, 1957, through September, 1958.

was available, temperatures undoubtedly were quite low. Only under such circumstances of very sparse cover does it seem probable that low temperatures influence local distribution of *B. brevicauda*. Similarly, high temperatures did not appear to exert any significant influence except perhaps in the old field. In all other areas at the level occupied by *B. brevicauda*, the temperatures apparently were moderated enough by the vegetation to prevent their being an important factor.

Interspecific Competition.—No obvious positive or negative influences of other species occurred. *B. brevicauda* was abundant in some areas in which *Sorex cinereus* was also abundant. In those areas in which *S. cinereus* was abundant, but in which *B. brevicauda* was absent or scarce, factors other than competition are more important. In the bog, spruce-birch-larch swamp and burn, the low available food supply appears to be responsible, while in the grass-sedge marsh (when it was inundated) standing water brought about an avoidance of the area on the part of *B. brevicauda*.

Predation Upon Voles.—Population densities were not higher in areas in which *Microtus pennsylvanicus* was abundant. Furthermore, *B. brevicauda* was often more abundant where *M. pennsylvanicus* did not occur (i.e., *P. fruticosa* area of the marsh). *B. brevicauda* was also abundant, however, in places in the marsh and old field in which *M. pennsylvanicus* was abundant. *M. pennsylvanicus*, therefore, did not appear to influence its distribution.

Conclusions.—*B. brevicauda* is not limited in its local distribution by any particular type of vegetation. It is found in all types ranging from entirely herbaceous to entirely woody. Areas with soil moisture lower than that required to keep the air in the burrows or in the humus saturated are not inhabited. Likewise, those areas in which the surface is inundated are avoided. Since *B. brevicauda* is unable to regulate evaporative losses to any extent, a relatively high humidity is required to reduce water losses when the animals are active. Any type of cover that allows the air to maintain a high humidity condition may be utilized. This can take the form of dense grass-like vegetation or a well-developed leaf mold.

Since *B. brevicauda* has a high rate of metabolism it requires a large intake of food. Areas in which the available food supply is low may be avoided regardless of the presence of other favorable conditions. This was demonstrated in the present work by the absence of *B. brevicauda* from the birch-larch swamp. This area appeared to have favorable conditions for *B. brevicauda* in all factors except food, the number of larger forms of invertebrates was very low. However, the presence of an abundant food supply is not the sole factor favoring the presence of the shorttail shrew. The old field (during the summer) and the inundated portion of the marsh both had greater amounts of available food than did other areas in which *B. brevicauda* was abundant. This species was very scarce in these situations, however. Unless other

factors are favorable, an abundant food supply thus has little apparent influence upon the local distribution of *B. brevicauda*.

The only obvious influence of cover is in areas in which the vegetation is extremely sparse. These areas are avoided during times of the year when temperature extremes are at a maximum. Sparse vegetation also results in low humidity conditions. Thus cover, humidity, and temperature are interacting factors. There seems to be little difference in abundance of *B. brevicauda* when one compares areas that differ in the number of fallen trees, stumps, and debris present. Within a given habitat, population densities may be somewhat higher where cover is more abundant owing to increased availability of homesites or shelter from temperature extremes, but this was not demonstrated in the present study.

Temperature apparently becomes a factor in local distribution only in those areas in which vegetation is sparse (e.g., denuded or with sparse herbaceous vegetation). The differences in temperature in other areas are not normally great enough to have any appreciable influence upon the local distribution of *B. brevicauda*.

The influence of other species upon the local distribution of *B. brevicauda* did not appear to be of major importance. Whenever such a relationship appeared possible, other factors were seen as more probable.

Sorex cinereus

The masked shrew occurs in a wide variety of situations within its range (Burt, 1948). It apparently prefers no particular type of vegetation since it is found in forested and grassy areas as well as in various intermediate types. Although not found in upland hardwoods in southern Michigan, *S. cinereus* occurs in this type of vegetation in northern Michigan (Burt, personal communication). Therefore, a negative response to such a vegetation type is not to be expected.

That moisture is a factor in its local distribution has been shown by Manville (1949), Pruitt (1953), and Townsend (1935). Manville (*op. cit.*) indicated that *S. cinereus* was more dependent upon a moist environment than was *Blarina brevicauda*. Cahn (1937) found that *S. cinereus* apparently avoided wet swamps in Ontario although it was abundant in areas bordering the swamps. As with *B. brevicauda*, the food of *S. cinereus* has a water content of 60 to 95 per cent which augments intake of free water.

Pearson (1947) found that *S. cinereus* had the highest rate of metabolism of any of the 13 species of small mammals he tested (including *B. brevicauda*). This necessitates a high intake of food in order to supply an ample source of energy if the animals are to maintain themselves.

The present study was primarily an attempt to determine the influence of moisture, temperature, and food upon the distribution of *S. cinereus*. It was also desired to obtain comparisons between the responses of this species and *B. brevicauda*.

Vegetation.—*S. cinereus* occurred in all general types of vegetation except the oak-hickory upland (Figs. 6 and 7). There was no significant difference in the distribution between the other areas. They were found in the drier portion of the hardwood swamp which is similar in physiognomy to the oak-hickory habitat. Thus, no selection or avoidance of woody or herbaceous plants nor physiognomy of the vegetation was apparent.

Cover.—There was no correlation between the amount of cover present in the woody areas (logs, brush, etc.) and the captures of *S. cinereus* (r_s , .47; P , .05 = .714). They were also abundant in areas entirely lacking such cover. Cover of this type, therefore, does not appear to be an important factor in the distribution of *S. cinereus*. They were also found in areas not having a leaf mold as well as in those where it was present.

Moisture.—*S. cinereus* occurred in areas with all degrees of moisture, except dry portions of the old field. Data from the marsh (during the months when it was partly inundated) showed that *S. cinereus* was most abundant where standing water was present (Fig. 8). The masked shrew thus differed markedly from the shorttailed shrew in this aspect. When no standing water was present *S. cinereus* was found in the areas that had previously had standing water. As has been noted, trap mortality of *S. cinereus* was high and most were killed by the trapping. The population was thus disturbed to a point where the summer data from the marsh are meager.

Food.—No correlation existed between the availability of the larger invertebrates and the distribution of *S. cinereus*. This species is probably able to utilize small food items such as ants, collembolans, and other small invertebrates. These forms are present in sufficient numbers in most areas to furnish an ample supply of food. Abundance of food likewise did not result in a larger population in any particular area. The *P. fruticosa* area of the marsh and the entire old field both had a considerable amount of available food (Fig. 4). These two areas were avoided by *S. cinereus*. Likewise, the oak-hickory, which was also avoided, had a greater available food supply than did several of the other areas in which *S. cinereus* was abundant.

Temperature.—As with *B. brevicauda*, temperature did not appear to play a significant role in the local distribution of *S. cinereus*. In

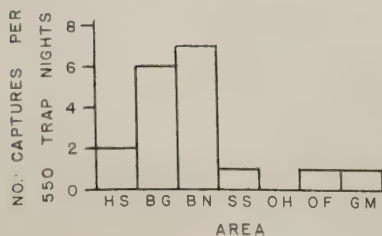


Fig. 6. — Relative abundance of *Sorex cinereus* in the seven habitats of the generalized study. Fall and winter trapping data combined. HS, hardwood swamp; BG, bog mat; BN, burn; SS, spruce-birch-larch swamp; OH, oak-hickory; OF, old field; GM, grass-sedge marsh.

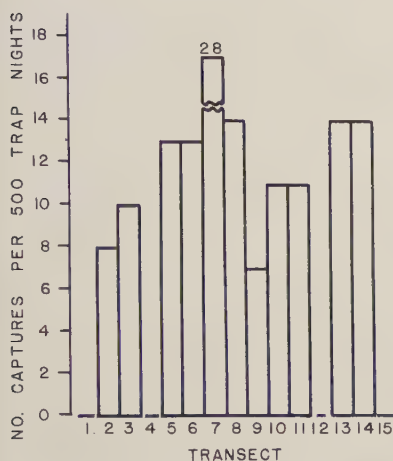


Fig. 7.—Transect captures of *Sorex cinereus*

areas in which a leaf mold or *Sphagnum* was present, the shrews were primarily active below the surface. Where such a cover was not present, as in the marsh, grasses or sedges normally covered the surface. In such areas where the shrews were active under the cover of vegetation or a leaf mold, the temperatures they encountered were relatively moderate (Fig. 5; Getz, in press). Although some activity may have occurred on the surface, *S. cinereus* was abundant in situations having the most extreme surface temperatures (i.e., bog mat and spruce burn). A further indication that low temperatures did not influence the distribution of *S. cinereus* was found in the spruce swamp. There was little cover in the form of a leaf mold in this habitat and the shrews were primarily active on the surface. Although temperatures were at times quite low on the surface, *S. cinereus* was abundant here. That relatively few individuals were captured in the old field is most likely a result of the combined effects of low humidity and temperature extremes.

Interspecific Competition.—No major influence upon the distribution of *S. cinereus* by other species was apparent. The absence of *S. cinereus* in the *P. fruticosa* area of the marsh and in the oak-

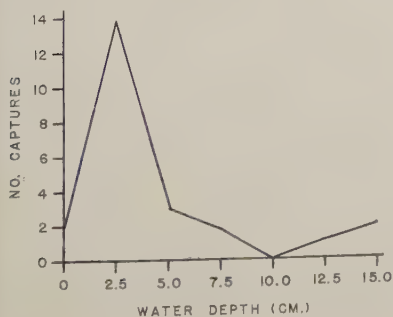


Fig. 8.—Relationship of captures of *Sorex cinereus* and depth of standing water in the marsh. Total captures during months standing water was present, October, 1957, through May, 1958.

hickory may have been in part a result of the high population densities of *B. brevicauda* in these areas. Both species were abundant in other areas, however, so that competition does not appear to be a primary factor involved in the local distribution of *S. cinereus*.

Conclusions.—The type or physiognomy of the vegetation has no apparent influence upon the local distribution of *S. cinereus*. In the more southern parts of its range it avoids upland hardwoods, but since this type of vegetation is inhabited in the more northern regions, factors other than the type of vegetation are probably involved.

As in the case of *B. brevicauda*, *S. cinereus* is restricted to moist situations. It was comparatively less abundant in the old field than was *B. brevicauda*, suggesting less tolerance to low humidity. In contrast to *B. brevicauda*, it is present in areas in which the surface is inundated.

S. cinereus is small and is able to utilize smaller food items than is *B. brevicauda*. Since the small invertebrates are quite abundant in almost all areas, food is not an important factor in the local distribution of *S. cinereus*.

Temperature differences had no obvious influence upon the local distribution of *S. cinereus* except in those areas in which the vegetation was very sparse. Such a situation, an old field, was present in this study, but it was also quite dry and this may have been a factor in its avoidance by *S. cinereus*.

In certain situations high population densities of *B. brevicauda* may result in fewer numbers or in the absence of *S. cinereus*. This does not appear to be a general factor, however, as both species occur in abundance in other situations.

DISCUSSION

The most important factor influencing the local distribution of *Sorex cinereus* and *Blarina brevicauda* is moisture. As has been found by Pruitt (1953, 1959), these species probably can permanently inhabit only those situations in which the air humidities approach saturation. *B. brevicauda* did not occur where standing water was present; *S. cinereus*, on the other hand, was abundant under such conditions. The difference in response to standing water could not be explained in the present study. *S. cinereus* is a more agile animal than is *B. brevicauda* (based on observations of the two species in captivity). This greater agility combined with a lesser body weight and longer tail, which facilitates balancing, may allow *S. cinereus* to run above the surface of the water on the leaves of the grasses and sedges. *B. brevicauda* is of more stocky build and less agile so that it probably cannot maneuver on the vegetation so easily.

Within situations having favorable moisture conditions, food appears to be the most important factor influencing the distribution of *B. brevicauda*. This species is absent from those areas having rela-

tively low food availability (in the form of larger invertebrates: beetles, snails, earthworms, etc.). *S. cinereus* was not so influenced by fewer numbers of such food items. Although the larger invertebrates were scarce in some habitats, the smaller forms (ants, collembolans, and spiders) were abundant in all. It is possible, therefore, that *S. cinereus*, owing to its smaller size (especially its small teeth), may be able to utilize smaller food items than can *B. brevicauda*. As a result there would be an adequate food supply in almost all situations.

The primary importance of cover appears to be its influence upon humidity. The main requirement is the presence of cover to maintain high humidity conditions, whether it be in the form of a leaf mold, moss, or vegetation (particularly graminoids). In areas where cover is sparse, humidity conditions may be unfavorable for part of the day during certain times of the year. Although some species of small mammals may alter their activity patterns so as to avoid short periods of unfavorable conditions (Getz, in press), this may not be possible for shrews. Owing to their high metabolic rates and the resulting necessity for large intakes of food, shrews probably have to remain active throughout the day and night to obtain sufficient quantities of food. As a result they could not permanently inhabit situations in which the humidity conditions become unfavorable for extended periods.

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Studies of the Byron Bog in Southwestern Ontario.

XII. A Study of the Population of Insects Emerging as Adults from Redmond's Pond in 1957¹

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ABSTRACT: Between March 23 and October 4, 1957, 13,159 adult insects were trapped in five tent-traps set out on the pond on water up to 3 ft. deep. The orders represented were Ephemeroptera (0.02%), Odonata (0.12%), Trichoptera (0.3%), Hemiptera (0.02%), Coleoptera (0.04%) and Diptera (99.5%). Midges of the family Chironomidae constituted 78.3% of the Diptera and Culicidae 21% of the Diptera. Other families of Diptera were Tipulidae, Ceratopogonidae, Dolichopodidae, Simuliidae, Tabanidae, Ephydriidae and Muscidae. Families of Coleoptera were Helodidae and Chrysomelidae. The numbers and seasonal occurrences, including times of maximum emergence, are reported for each species.

In 1956 a collection of insects emerging from Redmond's Pond in the Byron Bog was made by trapping the insects in a floating tent-trap (Judd, 1958b). In 1957 a second study of the aquatic insects of Redmond's Pond was undertaken using five tent-traps set out on the pond. The present paper is a report on this study.

Acknowledgment.—The writer gratefully acknowledges the assistance of Mr. R. B. Catalan who aided throughout the summer of 1957 in collecting insects from the traps, in sorting and counting specimens and in recording data. Much of the data were assembled while the writer held a Summer Research Associateship of the National Research Council in 1957.

DESCRIPTION OF COLLECTION SITES

Redmond's Pond is situated in the northwest corner of the Byron Bog as shown on the map accompanying the description of the bog (Judd, 1957b). It is completely surrounded by the sphagnum mat which forms the center of the bog, and the bushes of leatherleaf, *Chamaedaphne calyculata*, which grow in the sphagnum, have their branches extending out over the water of the pond. In 1957 the pond was 240 feet long in the north-south direction and 160 feet wide at its greatest diameter (Fig. 1). The water depth remained almost constant during the summer and nowhere on the pond was it more than five feet. The bottom of the pond was covered with loose, brown peat. No attempt was made to measure the depth of the peat in 1957, but Woolverton (1900) found that the peat in the center of the Byron Bog was at least 60 feet deep. The surface of the pond was devoid of vegetation in 1957 except in small bays around the circumference.

¹ Contribution from the Department of Zoology, University of Western Ontario; a project supported by funds from the Ontario Research Foundation and an operating grant from the National Research Council.

On March 14, 1957 the pond was still completely covered by ice and by March 16 all the ice had melted away. Thereafter light shell ice formed on the water at the edge of the pond on cooler nights during March. On March 23 traps 1, 3 and 5 were set in position at locations around the edge of the pond, and on March 30 traps 2 and 4 were set in position in the deeper water toward the center of the pond (Fig. 1). Location "6" on the map is the site at which the single trap was anchored in 1956. Each trap was kept in its one position during the season by a rope anchored at one end to bricks on the bottom of the pond and stapled at the other end to the side of the trap. The inside dimensions of each trap were 2 ft. x 2 ft. so the trap covered 4 sq. ft. of water surface. The traps were kept in position until October 4 when collections were discontinued. Thin shell ice formed at the edge of the pond on that day.

Trap 1 was located in a small bay in the north-east corner of the pond surrounded by bushes of leather leaf and on water 2 feet deep. Rooted vegetation in and around the trap comprised Spatterdock, *Nuphar advena* (Ait) Ait. f. and Bladderwort, *Utricularia vulgaris* L. Floating on the surface was a sparse accumulation of fronds of Duckweed, *Lemna minor* L. and Water Flax-seed, *Spirodela polyrhiza* (L.) Schleid. Trap 2 was located in the center of the pond on water 3 feet deep where there was no vegetation. Trap 3 was located at the west edge of the pond in water 2 feet deep where rooted plants of *Utricularia vulgaris* were present and a few fronds of *Lemna minor* and *Spirodela polyrhiza* floated at the surface. Trap 4 was toward the center of the pond on water 3 ft. deep

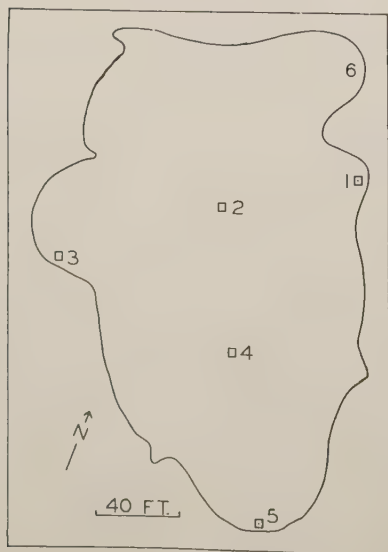


Fig. 1.—Map of Redmond's Pond showing location of the five tent-traps (1-5). Location "6" is the site of the trap on the pond in 1956.

where there was no vegetation. Trap 5 was at the south end of the pond over a floating shelf of moss extending from the edge of the pond. Thus the trap was floating in water 1 foot deep over a mat of sphagnum and other mosses and had in and around it a heavy growth of rooted plants of *Nuphar advena* and *Utricularia vulgaris*.

METHODS

Each day until October 4 the insects caught in each trap were collected. One side of the trap was raised above the surface of the water and an aspirator was passed into the trap and small insects were sucked up into it. Larger insects, such as dragon-flies, were picked from the lower surface of the screen with the fingers. The insects so collected were put into a killing jar and taken to the laboratory for sorting, counting, pinning (or preserving in fluid) and labeling.

The various groups of insects were identified by the following taxonomists, who, unless otherwise noted, are staff members of the Entomology Research Division, United States Department of Agriculture (USDA) or of the Entomology Research Institute, Canadian Department of Agriculture (CDA): C. P. Alexander, University of Massachusetts, Amherst (Tipulidae), W. J. Brown, CDA (Coleoptera), J. G. Chilcott, CDA (Ephydriidae, Muscidae), D. M. Davies, McMaster University, Hamilton, Ontario, (Simuliidae), F. P. Ide, University of Toronto (Ephemeroptera), L. A. Kelton, CDA (Hemiptera), J. F. McAlpine, CDA (Tabanidae), A. Stone, USDA (Culicidae), J. R. Vockeroth, CDA (Dolichopodidae), E. M. Walker, Royal Ontario Museum, Toronto (Odonata), G. B. Wiggins, Royal Ontario Museum (Trichoptera), W. W. Wirth, USDA (Ceratopogonidae, Chironomidae).

All specimens are retained in the collections of the Department of Zoology, University of Western Ontario except as noted (USNM—United States National Museum, CNC—Canadian National Collection, ROM—Royal Ontario Museum) in the following account.

ACCOUNT OF TOTAL CATCH

The numbers of the insects in the six orders collected from the traps are presented in Table I. During the whole period that the traps were in operation, March 23 to October 4, 13,159 insects were trapped. Most of the insects are species whose larvae or nymphs live submerged and whose adults emerge from the water, but a few are insects that dwell on emergent aquatic vegetation. The great majority (99.5%) were Diptera and among these the Chironomidae predominated (78.3%). Next in point of numbers (21%) were the Culicidae. The other families of Diptera were present in much smaller numbers.

The most productive site was Trap 5, yielding more than half the total catch. It was in shallow water over a mat of moss and surrounded by aquatic vegetation. The least productive sites were

TABLE I.—Number of insects of the six orders collected in the traps

Group	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5		% of Diptera	No.	% of Total
	No.	%	No.	%	No.	%	No.	%	No.	%			
Ephemeroptera	0	0	0	0	1	50	0	0	1	50		2	0.02
Odonata	0	0	0	0	1	7	1	7	13	86		15	0.12
Trichoptera	1	2	2	4	0	0	8	22	27	72		38	0.30
Hemiptera	0	0	0	0	2	100	0	0	0	0		2	0.02
Coleoptera	1	25	0	0	2	50	0	0	1	25		4	0.04
Diptera													
Tipulidae	1	100	0	0	0	0	0	0	0	0	0.01	1	0.01
Chironomidae	1,012	10	1,007	10	647	7	519	5	7,068	68	78.30	10,253	78.30
Ceratopogonidae	8	17	3	6	14	29	17	37	5	11	0.47	47	0.47
Culicidae	394	14	296	11	916	33	183	7	986	35	21.00	2,775	21.00
Dolichopodidae	0	0	0	0	0	0	0	0	2	100	0.02	2	0.02
Simuliidae	5	72	1	14	0	0	0	0	1	14	0.07	7	0.07
Tabanidae	0	0	0	0	0	0	1	100	0	0	0.01	1	0.01
Ephydriidae	0	0	0	0	0	0	0	0	11	100	0.11	11	0.11
Muscidae	0	0	0	0	0	0	0	0	1	100	0.01	1	0.01
Total Diptera	1,420	11	1,307	10	1,577	12	720	5	8,074	62	100.00	13,098	99.50
TOTALS	1,422	11	1,309	10	1,583	12	729	5	8,116	62		13,159	100.00

at Traps 2 and 4 where there was no vegetation. Traps 1 and 3, in which some vegetation was present, were more productive than Traps 2 and 4 but much less so than Trap 5. The area of water surface covered by each trap was 4 sq. ft., so the total area from which the insects were collected was five times this area, 20 sq. ft. Over the whole season 13,159 insects were trapped, an average yield of 658 insects per sq. ft. The average catch per sq. ft. for the five traps, respectively, was 356, 327, 396, 182, 2029 insects. The first insects emerged on April 21 and the last on October 4. The time of maximum emergence was the first week of June owing to large emergences of *Calopsectra* sp. and *Chaoborus flavicans* (Fig. 4).

The proportionate numbers of insects of the six orders trapped in 1957 (Table I) were closely similar to those caught in the single trap in 1956 (Judd, 1958b).

ACCOUNT OF SPECIES COLLECTED

The five bracketed numbers following the name of each species are the numbers of that species trapped, respectively, in the five traps.

EPHEMEROPTERA

BAETIDAE

Callibaetis sp.—2 mayflies (0 : 0 : 1 : 0 : 1); August 28.

ODONATA

COENAGRIIDAE

Enallagma ebrium (Hagen)—1 ♀ (0 : 0 : 0 : 0 : 1); June 10. This species was also trapped in shallow, weed-choked water in the Dundas Marsh (Judd, 1953), a habitat similar to that at Trap 5 where the specimen emerged in Redmond's Pond. Walker (1953) reports that sphagnum-bog ponds are unfavorable to this species.

Enallagma boreale Selys—2 ♂ ♂, 3 ♀ ♀ (0 : 0 : 1 : 0 : 4); May 24- June 7. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b). Its period of emergence in the bog is in accord with the estimate of Walker (1953) that its earliest recorded date of emergence is May 16 and that although it is sometimes very abundant in June, its numbers are already dwindling before the end of this month.

Enallagma hageni (Walsh)—1 ♀ (0 : 0 : 0 : 1 : 0); June 24. Walker (1953) notes that this species is tolerant of acid waters.

AESCHNIDAE

Anax junius (Drury)—1 dragon-fly (0 : 0 : 0 : 0 : 1); August 4. This species was trapped also on August 9 in 1954 at London (Judd, 1957a). Walker (1958) reports that its main period of emergence begins early in August.

LIBELLULIDAE

Sympetrum vicinum (Hagen)—2 ♂ ♂, 5 ♀ ♀ (0 : 0 : 0 : 0 : 7); July 26-August 18. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b). Its emergence from the shallow water at Trap 5 is in accord with the report by Judd (1953) that it emerged from shallow water in the Dundas Marsh.

TRICHOPTERA

LEPTOCERIDAE

Trienodes nox Ross—2♂♂ (0 : 0 : 0 : 0 : 2) (ROM) June 27, August 14. Ross (1944) records this species from Ontario.

Trienodes sp.—2♀♀ (0 : 0 : 0 : 0 : 2) (ROM); June 20, August 10.

Oecetis inconspicua (Walker)—14♂♂, 10♀♀ (1 : 0 : 0 : 1 : 22) (ROM); June 14–September 2, maximum July 30 (4 insects), Figure 2. This species was trapped also in 1956 both from Redmond's Pond (Judd, 1958b) and South Walker Pond (Judd, 1960) near London. The preponderance of this species in Trap 5 may possibly be explained by the fact that the larvae of *O. inconspicua* are predaceous (Ross, 1944) and would thus find abundant food in the large concentration of other insects at this site.

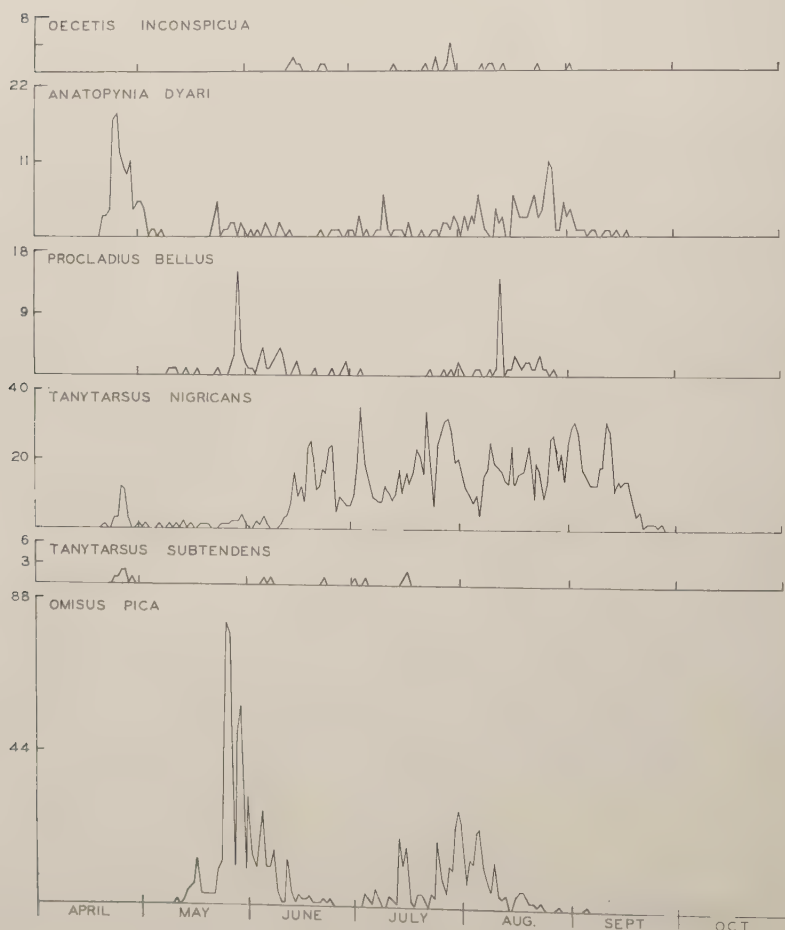


Fig. 2.—Periods of emergence of adult insects

PHRYGANEIDAE

Agrypnia vestita (Walker)—1 ♀ (0 : 0 : 0 : 0 : 1) (ROM); June 4. Ross (1944) reports that this species occurs in lakes and marshes.

Banksiola crotchii (Banks)—7 ♀ ♀ (0 : 1 : 0 : 6 : 0) (ROM); June 20-July 9. This species emerged only in the open water at Traps 2 and 4. Ross (1944) records it from Canada in British Columbia.

HYDROPSYCHIDAE

Cheumatopsyche sp.—1 ♀ (0 : 0 : 0 : 1 : 0) (ROM); August 26.

HYDROPTILIDAE

Hydroptila perditia Morton—1 ♂ (0 : 1 : 0 : 0 : 0) (ROM); June 21. Ross (1944) gives records from Ontario and Judd (1957a) trapped this species at London.

HEMIPTERA

SALDIDAE

Saldula opacula (Zett.)—2 bugs (0 : 0 : 2 : 0 : 0); June 12, 18. The shore bugs are reported by Usinger *et al.* (1956) to inhabit situations including springs and bogs. *S. pallipes* was trapped on Redmond's Pond in 1956 by Judd (1958b).

COLEOPTERA

HELODIDAE

Scirtes tibialis Guérin—2 beetles (1 : 0 : 1 : 0 : 0); July 22, August 4. Usinger *et al.* (1956) refer to reports that the larva of this beetle feeds on duckweed and that the pupa forms on the same plant. Duckweed was found on Redmond's Pond in 1957 particularly at Traps 1 and 3 where the beetles were trapped. The time of emergence of the two beetles is in accord with the report of Kraatz (1918) that the adults become increasingly abundant up to the latter part of July, after which there is a rapid decline until the last week of August.

Cyphon variabilis Thunb.—1 beetle (0 : 0 : 1 : 0 : 0); June 5. Usinger *et al.* (1956) give records of larvae of *Cyphon* occurring in ponds and in wet moss and under stones around springs.

CHRYSOMELIDAE

Longitarsus sp.—1 beetle (0 : 0 : 0 : 0 : 1); April 21. Judd (1960) records trapping *Longitarsus* sp. on South Walker Pond in 1956.

DIPTERA

TIPULIDAE

Limnophila laricicola Alex.—1 cranefly (1 : 0 : 0 : 0 : 0); May 28. Alexander (1942) reports that this species is characteristic of sphagnum bogs and gives records of its occurrence in some of the northern United States.

CHIRONOMIDAE

Pentaneura monilis (L.)—4 ♂ ♂ (2 : 1 : 0 : 0 : 1); June 1, 28, July 12, August 8. This species was trapped in much larger numbers than in Redmond's Pond both on the Dundas Marsh (Judd, 1953) and on South Walker Pond (Judd, 1960).

Pentaneura spp.—1 ♂, 15 ♀ ♀ (4 : 1 : 5 : 0 : 6); May 14-August 4.

Pelopia stellata (Coq.)—5 ♂ ♂, 4 ♀ ♀ (0 : 0 : 0 : 2 : 7); June 10-July 8, August 21. This species was also trapped in 1956 in the water of the hypolimnion at South Walker Pond (Judd, 1960).

Clinotanytus thoracicus (Lw.)—1 ♀ (0 : 0 : 1 : 0 : 0); June 14. This species was also trapped in 1956 from South Walker Pond (Judd, 1960).

Anatopynia dyari (Coq.)—178 ♂♂, 109 ♀♀ (31 : 31 : 52 : 26 : 147); April 21-September 18, maxima April 25, August 27 (18, 11 insects), Figure 2. This species was also trapped from pools at London (Judd, 1957a), from South Walker Pond (Judd, 1960) and from Redmond's Pond (Judd, 1958b) when the times of emergence were in June.

Procladius culiciformis (L.)—6 ♀♀ (0 : 1 : 0 : 2 : 3); May 27-August 10. This species was trapped also in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960).

Procladius bellus (L.)—52 ♂♂, 55 ♀♀ (7 : 13 : 26 : 17 : 44); May 10-August 28, maxima May 30, August 13 (15, 14 insects), Figure 2. This species was trapped also in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960) being well-distributed through the season at all three locations.

Hydrobaenus sp.—1 ♀ (0 : 0 : 0 : 0 : 1); April 22.

Polypedilum sp.—3 ♂♂ (0 : 2 : 1 : 0 : 0); June 6, 21, July 11.

Tanytarsus nigricans (Joh.)—853 ♂♂, 849 ♀♀ (70 : 380 : 217 : 281 : 754); April 21-September 27, Figure 2. The emergence of this species remained high during the season after an upsurge in June. It was also trapped in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960).

Tanytarsus subtendens Townes—15 ♂♂ (8 : 0 : 0 : 7 : 0); April 24-July 17, Figure 2. This species was also trapped in 1956 from Redmond's Pond (Judd, 1958b).

Tanytarsus punctipes (Wied.)—258 ♀♀ (6 : 233 : 1 : 2 : 16); May 14-September 23, maximum August 31 (31 insects), Figure 3. Most of these midges emerged in the open water at Trap 2. The species was trapped also in 1956 from Redmond's Pond (Judd, 1958b) where it also showed a maximum emergence at the end of August. It was found also at South Walker Pond in 1956 (Judd, 1960).

Omisus pica Townes—448 ♂♂, 499 ♀♀ (474 : 3 : 5 : 1 : 464); May 11-September 5, maxima May 26, July 31 (81, 28 insects), Figure 2. This species was also trapped in 1956 on Redmond's Pond (Judd, 1958b) when it also showed two peaks of emergence, one in spring and the other later in the summer. Its heavy emergence in Traps 1 and 5 indicates that the larvae dwell in shallow water with vegetation.

Tendipes riparius (Meigen)—11 ♂♂, 20 ♀♀ (2 : 0 : 0 : 0 : 29); April 24-May 16, maximum April 26 (6 insects), Figure 3. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b) where it emerged also later in the season.

Tendipes dux (Joh.)—23 ♂♂, 33 ♀♀ (2 : 14 : 0 : 0 : 40); May 8-August 12, maxima May 9, July 22 (3, 4 insects), Figure 3. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b) and at London (Judd, 1957a) and South Walker Pond (Judd, 1960).

Tendipes nervosus (Staeger)—114 ♂♂, 237 ♀♀ (45 : 105 : 43 : 8 : 150); April 30-September 9, maxima May 1, July 3 (17, 37 insects), Figure 3. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b).

Glyptotendipes lobiferus (Say)—179 ♂♂, 72 ♀♀ (197 : 1 : 0 : 0 : 53); April 4-July 14, maxima April 28, May 24 (11, 74 insects), Figure 3. This species was also trapped commonly in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960). Its heavy emergence in Traps 1 and 5 on Redmond's Pond indicates that the larvae dwell in shallow water about vegetation.

Glyptotendipes brachialis (Coq.)—47 ♂♂, 43 ♀♀ (2 : 51 : 3 : 31 : 3); May 8-September 14, maximum June 26 (6 insects), Figure 3. This species was also trapped at London (Judd, 1957a) and South Walker Pond (Judd, 1960) where it likewise showed a maximum emergence at the end of June. In Redmond's Pond it emerged mostly in the open water at Traps 2 and 4.

Microtendipes pedellus (DeGeer)—59 ♂♂, 14 ♀♀ (4 : 0 : 4 : 12 : 53); April 28-September 1, maximum July 10 (5 insects), Figure 3. This species was also trapped on South Walker Pond (Judd, 1960).

Tendipes sp.—39 ♀♀ (2 : 37 : 0 : 0 : 0); June 24-September 22.

Calopsectra sp.—167 ♂♂, 5,839 ♀♀ (156 : 134 : 289 : 130 : 5,297); April 24-October 4, maxima April 25, May 31, July 6 (97, 369, 291 insects), Figure 4. These small, green midges emerged throughout the season. Their preponderance at Trap 5 indicates that the larvae dwell about vegetation in shallow water.

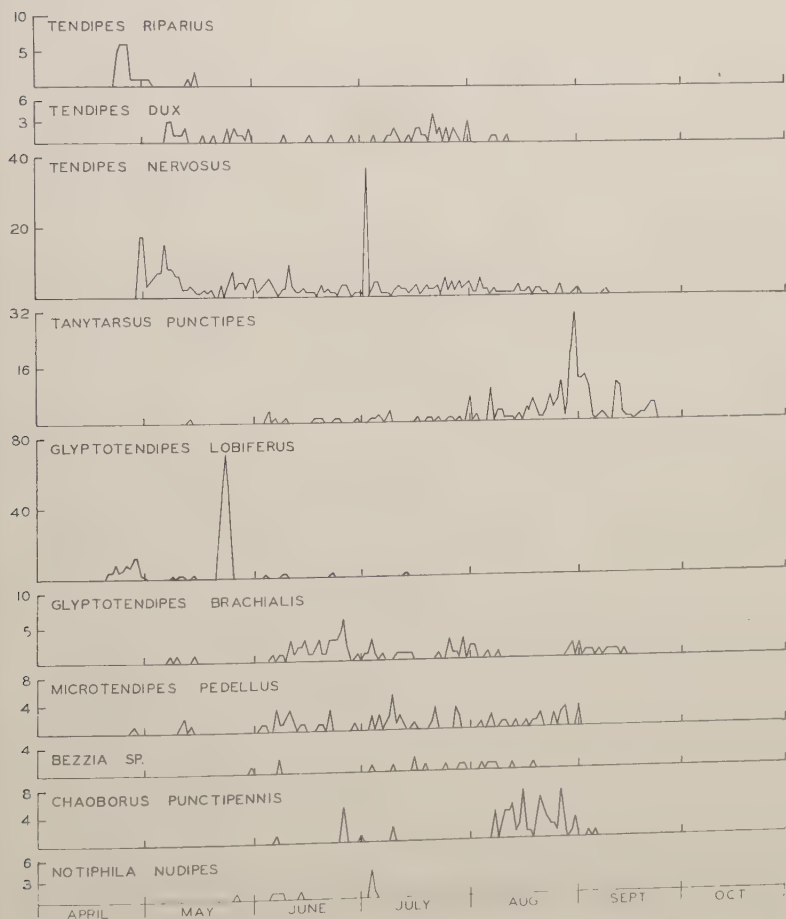


Fig. 3.—Periods of emergence of adult insects

CERATOPOGONIDAE

Alluaudomyia bella (Coq.)—1 ♀ (0 : 0 : 0 : 1 : 0); August 24. Larvae of this species have been found by Thomsen (1937) in algae, dead leaves and mud from ponds and swamps.

Culicoides (?*piliferus* R. and H.) (USNM)—1 ♀ (0 : 0 : 1 : 0 : 0); June 2. *C. piliferus* was trapped also in June on South Walker Pond in 1956 (Judd, 1960).

Atrichopogon sp.—2 ♂ ♂, 7 ♀ ♀ (3 : 0 : 0 : 6 : 0); June 12-26, August 26-31. The period of emergence recorded here for *Atrichopogon* is similar to that found by Judd (1960) at South Walker Pond where the flies emerged in late June and July and again in August and September.

Bezzia sp.—5 ♂ ♂, 12 ♀ ♀ (0 : 0 : 12 : 2 : 3); May 31-August 12, Figure 3. Midges of this species were also trapped at South Walker Pond (Judd, 1960).

Other Heleidae—19 midges (5 : 3 : 1 : 8 : 2); May 31-September 11.

CULICIDAE

Chaoborus flavicans (Meigen)—1,475 ♂ ♂, 1,225 ♀ ♀ (394 : 263 : 902 : 170 : 971); April 23-September 27, maxima April 27, June 5, July 31 (83, 289, 34 insects), Figure 4. This species was trapped also in 1956 on Redmond's Pond (Judd, 1958b) when it likewise showed its maximum emergence in June. Its preponderance at Traps 1, 3 and 5 indicates that the adults emerge mainly from shallow water. The species was trapped at London (Judd, 1957a) and South Walker Pond (Judd, 1960).

Chaoborus punctipennis (Say)—45 ♂ ♂, 30 ♀ ♀ (0 : 33 : 14 : 13 : 15); June 7-September 6, maximum August 27 (7 insects), Figure 3. Only one specimen was trapped on Redmond's Pond in 1956 (Judd, 1958b). Most of the adults emerged from the more open water at Traps 2 and 4. This species was also trapped at London (Judd, 1957a) and at South Walker Pond (Judd, 1960).

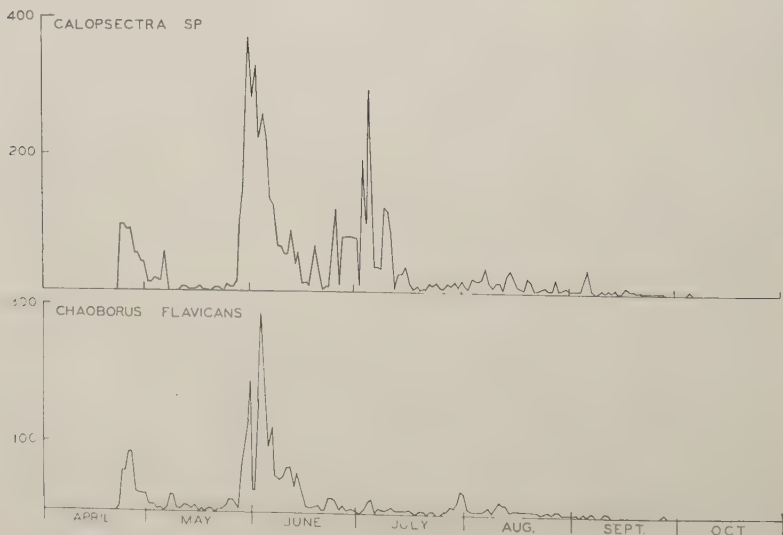


Fig. 4.—Periods of emergence of adult insects

DOLICHOPODIDAE

Dolichopus albiciliatus Lw.—1 ♀ (0 : 0 : 0 : 0 : 1) (CNC); June 7. Several other species of *Dolichopus* have been trapped from bodies of water in the vicinity of London (Judd, 1957a and 1960).

Gymnopternus barbatulus Lw.—1 ♀ (0 : 0 : 0 : 0 : 1) (CNC); July 10. This species was also trapped in July, 1954 from a pool at London (Judd, 1957a).

SIMULIIDAE

Simulium vittatum Zett.—1 ♂, 6 ♀ ♀ (5 : 1 : 0 : 0 : 1); June 11-September 6. This species was collected also in 1956 in the Byron Bog by sweeping the bushes in the *Chamaedaphnetum calyculatae* association which surrounds Redmond's Pond (Judd, 1957c). Its first emergence in the trap in 1957, June 11, was eighteen days earlier than the date of its first collection, June 29, in the sweeping in 1956.

TABANIDAE

Chrysops montana O.S.—1 deer-fly (0 : 0 : 0 : 1 : 0); June 4. This species was not among the tabanids collected in the Byron Bog in 1956 (Judd, 1958a). It has been recorded at Algonquin Park in Ontario where it was first found in flight on June 16 (Davies, 1959).

EPHYDRIDAE

Notiphila nudipes Cresson—2 ♂ ♂, 9 ♀ ♀ (0 : 0 : 0 : 0 : 11) (5, CNC); May 27-July 5, Figure 3. Berg (1949) found larvae of *N. loewi* on the roots of *Potamogeton* and McGaha (1952) found the same species associated with flowers of the water-lilies *Nymphaea odorata* and *N. tuberosa*. In Redmond's Pond *N. nudipes* may have been associated with spatter-dock, *Nuphar advena*, for all the flies emerged in Trap 5 which had this plant in it.

MUSCIDAE

Coenosia tigrina Fab.—1 fly (0 : 0 : 0 : 0 : 1); July 28. Under the subfamily Coenosiinae Usinger *et al.* (1956) list a few species of flies with aquatic larvae but do not include any in the genus *Coenosia*.

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The Comparative Morphology of the Definitive Swim Bladder in the Catostomidae

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ABSTRACT: The definitive swim bladder of the Catostomidae has been described and its variations noted. It is characteristically the two-chambered type found in cypriniform fishes in general and described by Tracy as Group 2.

The anterior chamber is encased in a tunica externa made up of special connective tissue fibers. This tunic is in two layers and the fibers of these layers are arranged at right angles to each other. It is proposed that this arrangement prevents over-expansion of the anterior chamber and thus maintains free range-of-motion for the Weberian ossicles.

The usual catostomid swim bladder is 35 - 45 per cent of the standard length of the individual. *Hypentelium*, adapted to riffle-type life, has the posterior chamber somewhat reduced. *Thoburnia* and *Pantosteus*, adapted to mountain streams, have the posterior chamber even more reduced.

The *Moxostoma* genus-group (*Moxostoma*, *Placopharynx*, *Megapharynx* and *Lagochilia*) has a three-chambered swim bladder. *Thoburnia* and *Hypentelium* are retained as separate genera of the Moxostomatini, being more primitive, although specialized, than the former.

INTRODUCTION

The Catostomidae is a family of teleost fishes, the suckers, in the cypriniform subdivision of the Ostariophysi. The catostomid fishes comprise some fifteen or seventeen genera and about a hundred species. For the most part they are limited to the fresh-waters of North America extending as far south as the Mexican Highlands. One genus, *Myxocyprinus*, however, is restricted to the fresh-waters of Central China from Szechwan to Fukien Provinces. A subspecies of the northern sucker, *Catostomus catostomus rostratus*, has invaded northeastern Siberia where it is to be found in the fresh-waters of the Kamchatka Peninsula and westward to the Lena River.

The typical cypriniform swim bladder is a two-chambered structure found in the body cavity (Fig. 1.). It lies immediately beneath the vertebral column in a retroperitoneal space above the abdominal viscera. A pneumatic duct passes along with the "service tissues" (vessels and nerves) between the two leaves of the dorsal mesentery and connects the posterior chamber of the swim bladder to the anterior gut. The anterior chamber is connected to the posterior by an inter-chamber duct and to the inner ear by an ossicle chain, the Weberian ossicles characteristic of the ostariophysine fishes. The definitive swim bladder of cypriniform fishes develops in a characteristic manner from an initial dorsal outgrowth of the gut wall (Nelson, 1959).

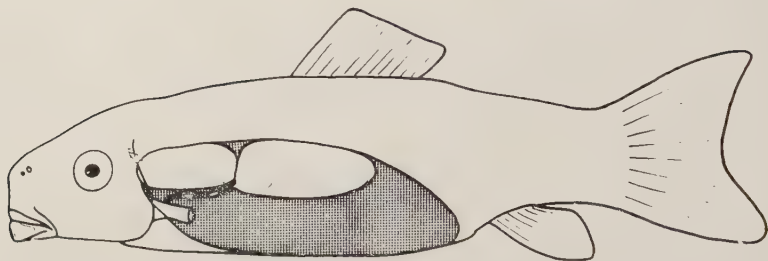


Fig. 1.—A schematic representation of the swim bladder *in situ* in *Catostomus commersoni*.

Since the swim bladder is usually a gas-filled structure, it plays an important role in the bouyancy of the individual fish. Different habitats place different requirements for survival upon the species, through the individual, and the swim bladder is responsive to the varying bouyancy requirements of different aquatic environments. Secondary roles are also possible for the swim bladder. In the Ostariophysi as a group, the anterior chamber has the added function of vibration reception and transmission to the membranous labyrinth to improve the sense of "hearing."

Within the Catostomidae the swim bladder has long been recognized as being a useful taxonomic tool because of its basic variation among the genus-groups. Hubbs (1930) used the number of chambers of the catostomid swim bladder as a primary character in his "Key to the Genera." Most recently, Robins and Raney (1956, 1957) made judgments as to the proper placing and synonymy of various species of catostomids on the same basis.

Many individual references to the swim bladders of individual species of catostomids have been made in the literature. No really complete or systematic morphology study of the swim bladder in the Catostomidae has been made to date, however. Dobbin (1941) gave very brief descriptions of the swim bladder in six species from five genera and figured three with outline sketches. The object of the present paper is to treat the swim bladder in the entire family in a systematic and more-or-less complete fashion as part of an over-all study of the Catostomidae. Fifty-two species, including representatives of all genera, have been examined in this study. All references to size or length are for standard length.

I express my thanks to the many people and institutions whose courtesies and help over the years have made this study possible. The majority of the specimens came from the Wisconsin Conservation Department, the University of Michigan Museum of Zoology, Chicago Natural History Museum, United States National Museum, Academy of Natural Sciences of Philadelphia and the Museum of Comparative Zoology. A number of separate items were made available to me by many persons, too numerous to mention individually, but whose action is much appreciated.

MORPHOLOGICAL FINDINGS

Chambers of the Swim Bladder.—The swim bladder in catostomid fishes may be either a two-chambered or three-chambered structure. The genus-group of *Moxostoma* is characterized by having the three-chambered type of swim bladder while all of the other genera have the two-chambered type. As presented in a previous paper (Nelson, 1959), the posterior chamber develops from the single chamber of the primitive swim bladder. The anterior chamber develops from a primordium which grows out from the anterior surface of this single chamber. Therefore, the swim bladder of catostomids is characterized as being in Tracy's (1911) Group 2.

The anterior and posterior chambers are inter-connected by an inter-chamber duct. This duct is located centrally on the opposing surfaces of the two chambers. It is distinctly separate from the pneumatic duct which opens into the lower anterior surface of the posterior chamber and connects the posterior chamber with the esophagus.

The third chamber of the moxostomids is connected to the second by a dorsal inter-chamber duct. This connection is a sometimes broader than a mere duct. The age at which the third chamber is acquired must be very early since even specimens of 2.5 cm have it.

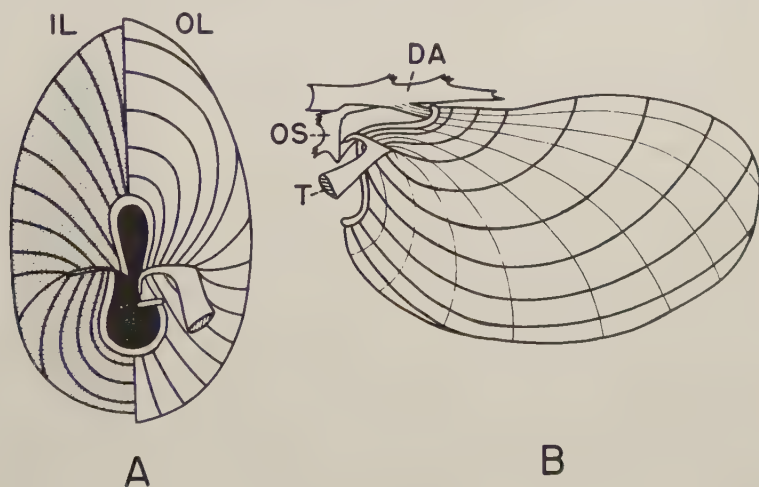


Fig. 2.—A schematic representation of the tunica externa of the catostomid swim bladder. A. Dorsal view with the anterior end at bottom. On the right side is depicted the lines of the direction of the fibers of the outer layer (OL). On the left side the outer layer has been removed to show the direction of the fibers of the inner layer (IL). The transformer process of the tripus is *in situ* attached to the outer layer. B. Lateral view to show the arrangement of the fibers of the inner and outer layers being at right angles to each other. The outer layer and transformer process (T) are attached to the suspensorium (OS) and the dorsal aorta (DA) gives off branch to the anterior chamber where the tunica interna is exposed at the central opening of the tunica externa.

In these very small specimens (2.5 and 3.8 cm), however, the third chamber is relatively smaller in size than usual.

Chamber Walls.—Fänge (1953) has presented a satisfactory resumé of the thinking concerning the layers of the swim bladder walls. In the catostomids the lumen of the swim bladder as a whole is lined by a continuous layer of epithelium. Next to this thin layer of epithelium is a layer of intermingled nonstriated muscle and connective tissue fibers. Three zones are apparent in this second layer: a) an inner zone primarily of connective tissue fibers; b) a thick zone which is the main area of the circular muscle fibers; and, c) an outer zone which is again mainly of connective tissue fibers. These two layers, epithelial and muscular, make up the tunica interna of the anterior chamber.

The tunica externa of the anterior chamber is formed of two thick layers of white connective tissue fibers. Each layer has all of its fibers arranged parallel so that one can produce long narrow splits in a layer with a dissecting needle. Figure 2 diagrams the manner in which the fibers of the inner and outer layers tend to always be coursing at right angles to each other (similar to the fibers of the intercostal and abdominal oblique musculature). Between the external and internal tunics of the anterior chamber is a loose connective tissue which allows these two tunics to be easily separated from one another.

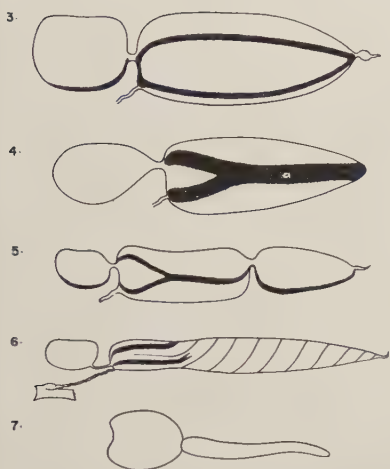
The posterior chamber has a single wall. This represents essentially a fusion of all layers into the single structure.

Posterior Extensions of the Posterior Chamber.—In certain genera of catostomids an extension arising from the posterior end of the posterior-most chamber is to be seen frequently. The lumen of this extension is continuous with that of the swim bladder proper. The posterior extension may have a simple tubular form or may be a bulbous enlargement, as if it were a miniature additional chamber.

The tubular type of posterior extension may be seen in *Carpionodes*, *Ictiobus*, *Megastomatobus*, *Moxostoma*, *Placopharynx* and *Cycleptus*. It may be short or of varying length, sometimes quite long as in *Moxostoma*. This tubular extension may be folded dorsally or ventrally; it may be straight posteriorly; or, it may be slightly convoluted. In all cases, however, it is usually embedded in the loose fascia filling the retroperitoneal space behind the swim bladder.

The bulbous type of extension, as far as the specimens available are concerned, is limited to the *Carpionodes* and *Moxostoma*. It is particularly evident in the former.

Longitudinal Bands.—Paired longitudinal bands occur on the lateral aspects of the posterior chamber wall of the catostomid swim bladder. These bands represent thickenings of the muscle or connective tissue fiber masses. In *Carpionodes* (Fig. 3), *Ictiobus*, *Megastomatobus*, *Cycleptus* (Fig. 6), and *Myxocyprinus* these longitudinal bands are muscular and doubled, one band dorsal and the other ven-



Figs. 3-7. Variation in swim bladders of catostomid fishes. 3. *Carpiodes cyprinus*, the type seen in the ictiobids, lateral view. 4. *Minytrema melanops*, lateral view. 5. *Moxostoma aureolum*, the type seen in the moxostomids, lateral view. 6. *Cycleptus elongatus*, lateral view. Note the triple spiralling of the two pairs of longitudinal bands. 7. *Thoburnia rhotodecta*, dorsal view. This is an example of the reduced type of swim bladder.

tral along the length of the posterior chamber converging towards the posterior end.

In *Catostomus*, *Erimyzon*, *Minytrema* (Fig. 4), *Moxostoma* (Fig. 5) and *Placopharynx* it appears as if these two bands (as seen above) have become variously fused so that there is a single longitudinal band on each side of the posterior chamber wall. The anterior end of this single band remains doubled to varying distance so as to have the appearance of a "Y" lying on its side. In *Catostomus*, however, it is not at all uncommon to find this band to be single throughout its entire length.

Spiral Character.—Several genera of catostomids exhibit a spiral "twisting" of the longitudinal bands of the posterior chamber in about ten per cent of the specimens. *Cycleptus* (Fig. 6) demonstrates this morphological character to the maximum degree. Here the anterior portion of the posterior chamber has the double muscular bands between which are longitudinal bands of thickened fibrous connective tissue. The latter produce internal ridges on the wall of the posterior chamber and are seen externally as grooves. In the posterior three-quarters of the posterior chamber the muscle bands are no longer apparent but the fibrous bands become spiralled into three complete turns.

The description above of the *Cycleptus* swim bladder is that for the definitive bladder. In a series of thirteen specimens, sizes 3.28 to 57.0 cm, the progressive development of this condition is demonstrated. In the youngest specimens the posterior chamber is simple and without any special modifications. Between the 6 to 9 cm sizes a single turn of fibrous bands may be seen along the entire length of the posterior chamber. The time at which the second and third turns appear cannot be ascertained in this limited series of specimens. The definitive bladder may at times also show the fiber bands twisted

along the entire length of the posterior chamber and one large specimen had only two instead of three turns.

In *Carpiodes* the spiralling extends into the bulbous posterior extension where it is quite marked. In *Moxostoma* the spiralling is limited to the third, the posterior-most chamber.

Those swim bladders of *Carpiodes* and *Ictiobus* which have this spiral character all have the direction of twist counter-clockwise when viewed from behind. The twist of the bands in *Megastomatobus*, *Cycleptus* and *Moxostoma* are all clockwise when viewed from behind.

Relationships of the Swim Bladder Length to the Standard Length of the Body.—The swim bladder of catostomid fishes occupies from a third to almost a half of the length of the body of the fish (Table I). It remains within the limits of the body cavity without extending posteriorly into the caudal portion of the body. In certain species the swim bladder is reduced in length to varying degrees. In *Thoburnia atripine* and *Hypentelium nigricans* the swim bladder is about a fourth of the body length. This is also true of the genus *Pantosteus* in general. In *Thoburnia rathoea* and *Pantosteus santa-anae* the

TABLE I.—Ratios of the swim bladder length/standard body length in the Catostomidae

	SB/SL $\times$ 100 = %	Number of Specimens:	
		Measured	Examined
Cycleptinae:	(43.9)		
<i>Cycleptus</i>	44.5	4	13
<i>Myxocyprinus</i>	42.6	2	2
Ictiobinae:	(39.7)		
<i>Carpiodes</i>	40.3	13	49
<i>Ictiobus</i>	38.3	5	9
<i>Megastomatobus</i>	39.0	2	31
Catostominae:			
Catostomini:	(35.0)		
<i>Catostomus</i>	35.2	26	126
<i>Chasmistes</i>	32.1	2	3
<i>Xyrauchen</i>	36.0	1	1
Moxostomatini:	(44.2)		
<i>Moxostoma</i> (less <i>mascoatae</i>)	44.1	14	52
<i>Placopharynx</i>	43.1	3	4
<i>Lagochila</i>	45.2	4	4
Erimyzonini:	(36.1)		
<i>Erimyzon</i>	35.5	8	20
<i>Minytrema</i>	38.3	5	36
"Reduced Swim Bladders":			
<i>Moxostoma mascoatae</i>	38.8	22	22
<i>Thoburnia atripinne</i>	28.1	9	9
<i>Hypentelium nigricans</i>	27.9	11	16
<i>Thoburnia rathoea</i>	17.2	14	16
<i>Pantosteus</i> (less <i>santa-anae</i>)	22.1	7	24
<i>Pantosteus santa-anae</i>	13.8	3	5
		155	444

swim bladder is even more reduced in length. In not a single specimen was the swim bladder found to be absent! (In *Thoburnia rathoea* the swim bladder is so small and buried in the fat and head-kidney tissue that it can be easily overlooked.) In all instances of reduced length, the posterior chamber undergoes the main reduction whereas the anterior chamber is relatively unaltered.

The question of possible shrinkage of the swim bladder during preservation was recognized as having possible consequences in this particular phase of this study and a simple experiment was performed to obtain some ideas about this matter. Fresh frozen specimens of *Catostomus commersoni* were used. During the removal of the swim bladder of the first specimen it was noted that the bladder contracted slightly when the pneumatic duct was transected. The second bladder was therefore filled with the fixing solution before removal from the body. Both swim bladders were removed from the fishes and placed into a calcium-formal fixing solution. After two and a half weeks they were transferred to seventy per cent ethyl alcohol for storage. In both cases the shrinkage of the anterior chamber was about fifteen per cent while that for the posterior chamber was about ten per cent of the freshly removed swim bladders. All of the shrinkage was completed by the time the specimens were placed in the alcohol since subsequent measurements for a period of three months showed no appreciable change. The SB/SL ratio changed from about forty per cent in the fresh state to about thirty-five per cent in the preserved state. This latter figure agrees well with the figure obtained from museum specimens. Thus it is assumed that all of the museum specimens have undergone the same amount of shrinkage uniformly and the ratios in Table I are those taken directly from the museum specimens.

When the swim bladder lengths of the various genera are plotted against standard lengths on plain graph paper, the resulting progression lines are essentially straight lines. The slope of these lines averages about twenty degrees. The few very large specimens (i.e. an adult *Myxocyprinus* of almost a meter in length) tend to flatten the end of the line towards a plateau.

DISCUSSION AND CONCLUSIONS

The Chambers of the Swim Bladder.—The two-chambered swim bladder is characteristic for the Catostomidae. Also, from both morphological and developmental studies it is apparent that the swim bladder seen in the Catostomidae is the same as for the other families of the cypriniform group of ostariophysines. This type of swim bladder has a posterior chamber with a single wall and is connected to the anterior gut via the pneumatic duct. The anterior chamber has a tunica interna which is continuous with the wall of the posterior chamber. About this inner tunic is consolidated a thick fibrous capsule, the tunica externa. The tunica externa is readily separated from the tunica interna by virtue of a loose connective tissue between them. The presence of a third chamber in the moxostomatids is a mor-

phological fact but its significance is enigmatic. This situation apparently rerresents a constriction of the normal posterior chamber since the pneumatic duct connects with the second chamber precisely as is the case with the posterior chamber of the two-chambered swim bladder. Also, the dorsal inter-chamber duct between the second and third chambers is on occasion large and fails to exhibit the characteristics usually associated with true ducts. It may be of systematic significance in that only those genera closely related as a *Moxostoma* group (*Moxostoma*, *Placopharynx*, *Megapharynx*, and *Lagochila*) possess this characteristic, whereas, other genera which exhibit structural affinity, Weberian apparatus and opercular series (Nelson, 1948, 1949), with this genus-group (*Thoburnia* and *Hypentelium*) have only the regular two-chambered bladder. Thus, we can agree with Robins and Raney (1956) and Bailey (1959) in considering all of the genera of the *Moxostoma* group as being subgenera of the genus *Moxostoma*, but retain *Thoburnia* and *Hypentelium* as separate and more primitive genera of the tribe Moxostomatini for the time being.

The literature has occasionally implied the presence of a third chamber on the swim bladder of *Minytrema*, and hence a close relationship to *Moxostoma*. In the present study the swim bladders of *Minytrema* and *Erimyzon*, Erymzonini, were consistent in being only two-chambered and well-rounded posteriorly; there is not the slightest indication of a possible posterior extension, much less an additional chamber. This type of swim bladder is morphologically much more similar to that of the Catostomini than to any other catostomid group.

Not a single specimen in this series of catostomids showed an absence of the swim bladder. The literature has reported occasionally that the swim bladder of *Thoburnia rathoeca* was lacking in adult specimens. This is probably based upon the anatomical fact that in this genus the swim bladder is much reduced and is frequently actually buried in the retroperitoneal tissue of the dorso-anterior portion of the body cavity.

The Tunica Externa of the Anterior Chamber.—The anterior chamber of the catostomid swim bladder appears to be specially adapted to function as a sound-wave receptor and to transmit these vibrations to the inner ear via the Weberian ossicle chain. The tunica externa forms a strong fibrous capsule about the gas-filled tunica interna and is attached to the Weberian apparatus, both at the ossa suspensoria and the transformator processes of the two tripuses. Because of the lack of adequate experiments with living fishes we may presume that the arrangement of the heavy connective tissue fibers of the two layers of the tunica externa at right angles to one another is a special adaptation for limiting possible over-expansion of the anterior chamber. (Expansion of the anterior chamber would occur with each ascent of the fish in its aquatic medium since the ascension would result in a reduction of the ambient pressure thus allowing an increased volume to the enclosed gases according to Boyle's Law. The posterior chamber, by means of the pneumatic duct and its valvular

mechanism in the wall of the esophagus, retains the bouyancy regulation function for the fish.) Too extensive expansion of the diameters of the anterior chamber would negate the functioning of the ossicle chain by limiting the range-of-motion of the normal articulations of the tripus and claustrum to the vertebrae.

Posterior Extensions.—Previously (Nelson, 1959), I noted that during the growth phase of the posterior chamber, a “nipple”-like posterior extension was present which retained the cytoarchitectural characteristics of the original diverticulum from the dorsal gut wall. These posterior extensions found in the definitive swim bladders may then be looked upon as resulting from an over-functioning of the organizing potential of the swim bladder determining mechanism to the extent that additional swim bladder structure is produced over and beyond the normal swim bladder morphology. This would be particularly true in the case of *Carpiodes* where the bulbous type of posterior extension gives the appearance of an additional, miniature chamber, even to the inclusion of the spiralling characteristic of the longitudinal bands.

Spiralling.—Except for *Cycleptus* this morphological character occurs sporadically (about ten %) rather than consistently. Moreover, it is a character which is not limited to a catostomid swim bladder but has been observed in other studies on the swim bladders of characins and gymnotids. How this “twisting” comes about (the swim bladder definitely does not rotate in place) and what it means in the economy of the fish is completely unknown.

Longitudinal Bands.—The thickening of muscle and/or connective tissue fibers into longitudinal bands represents a specialization in the swim bladders of the Catostomidae. The functional significance of these bands is not apparent from these studies but requires physiological experimentation with living material. We can, however, presume that the double condition seen in the genera of the subfamilies Cycleptinae and Ictibobinae represent the simpler and more primitive condition. The partially fused “Y” or completely fused single bands found in the Catostominae would then represent an increase complexity of morphology and thus place them at a higher systematic level.

Relationships of the Swim Bladder Length to the Standard Length of the Body.—A number of investigators have noticed that a fresh-water fish which is habitually suspended in the water medium possesses a swim bladder which is about seven per cent of the total body volume. The majority of the catostomid fishes can be classed in this category, albeit they are usually suspended just above the bottom. The small variation of the SB/SL ratios from thirty-five to forty-five per cent reflects only the differences in depth and width of the various swim bladders.

On the other hand, the genus *Hypentelium* is adapted to the more turbulent conditions of stream riffles while the genus *Thoburnia* is adapted to the swifter flowing waters of the mountain streams of the

Alleghenies in eastern North America and the genus *Pantosteus* similarly to the mountain streams of the Rockies in western North America. Apparently the species *Moxostoma mascotae* in the Highlands of Mexico parallels *Hypentelium* (Robins and Raney, 1957). In a series of twenty-two specimens of *M. mascotae* in two lots from the Rio Ameca and Rio Mascota, the SB/SL ratio is about thirty-eight per cent as compared to about forty-three per cent found in the *Moxostoma* group in general. *Thoburnia atripinne* and *Hypentelium nigricans* both have ratios of twenty-eight per cent. The genus *Pantosteus* is similar. In all of these forms, the bouyancy controlling portion of the swim bladder (the posterior chamber) is the part mainly reduced and these forms are able thereby to maintain themselves better in position despite the faster flowing waters of their habitats. The acme of this specialization to swift waters is to be seen in the species *Thoburnia rathoeca* and *Pantosteus santa-anae* where these ratios are much smaller.

The progression line of the plotted swim bladder lengths against the standard lengths of the body lead to two interesting conclusions. The fact that this line is essentially a straight line demonstrates that the growth of the swim bladder in relation to the growth of the body length is of the orthometric type. The fact that the slope of this line is approximately twenty degrees indicates that the SB/SL ratio begins and remains somewhere between thirty-five and forty per cent.

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Distribution of Some Mexican Fungi in North America

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ABSTRACT: When North America is divided into eight floristic regions roughly correlated with the distribution of woody angiosperms and conifers, a noticeable correspondence is found with the distribution of Polyporales. Twenty-seven species of Mexican Thelephoraceae and thirty-seven species of Mexican Polyporaceae are compared with reports of these same species from the other North American regions. By means of such reports, the affinities of these regions with Mexican mycota is shown.

Any attempt to discuss the geographical distribution of fungi is severely limited by the distressing lack of regional monographs and collections, by misinterpretations, and the erratic seasonal appearance of many species. When attempting to plot the distribution of saprobic fungi, these factors are especially intensified. Nevertheless, we have undertaken a modest discussion of the distributional affinities of some Mexican Thelephoraceae and Polyporaceae in relation to North America as a whole.

Bisby (1933; 1943) has reviewed the literature of fungus geography until 1943; the majority of the geographical studies have been upon plant pathogens, particularly those attacking crop plants. The few reports that exist on the distribution of saprobic fungi, such as those of Overholts (1939) and Lange (1934), have been chiefly concerned with North American and European fungi. Bisby (1933) and Lange are agreed that probably less distinction exists between temperate species of the eastern and western hemispheres than between those from northern and southern regions. Such studies as those of Bisby, Reichert (1921), and Sharp (1948) represent the very few reports on the distribution of tropical and subtropical species. No doubt, this represents a lack of knowledge of tropical forms rather than a lack of interest. Comparisons of tropical and subtropical species with those of temperate regions should prove to be of utmost interest as more information is accumulated through additional collections from warmer regions.

Fully cognizant of the difficulties mentioned, we have compared sixty-two species of Mexican fungi with distributional reports of various authors, primarily Burt (1914-1926), Murrill (1907; 1912; 1915), and Overholts (1953). These Mexican specimens were collected by us, and, in many cases, checked by recognized authorities. The taxonomic account of these fungi appears elsewhere (1960).

For convenience we have divided North America into eight regions (Fig. 1). These regions correspond roughly to the distribution of hardwoods and conifers — based primarily on Harshberger's work as shown in the maps of Goodall and Darby (1953). In many instances these regions also follow natural geographical or physiographical divisions; in others it has been more practicable to follow political boun-

daries. Further refinement and shifting of regional lines is both inevitable and desirable. Certain areas, *e.g.*, the New Mexico and Arizona highlands, assigned to a given region, may well be considered to belong to another. Similarly, the Gulf Coast which is here included

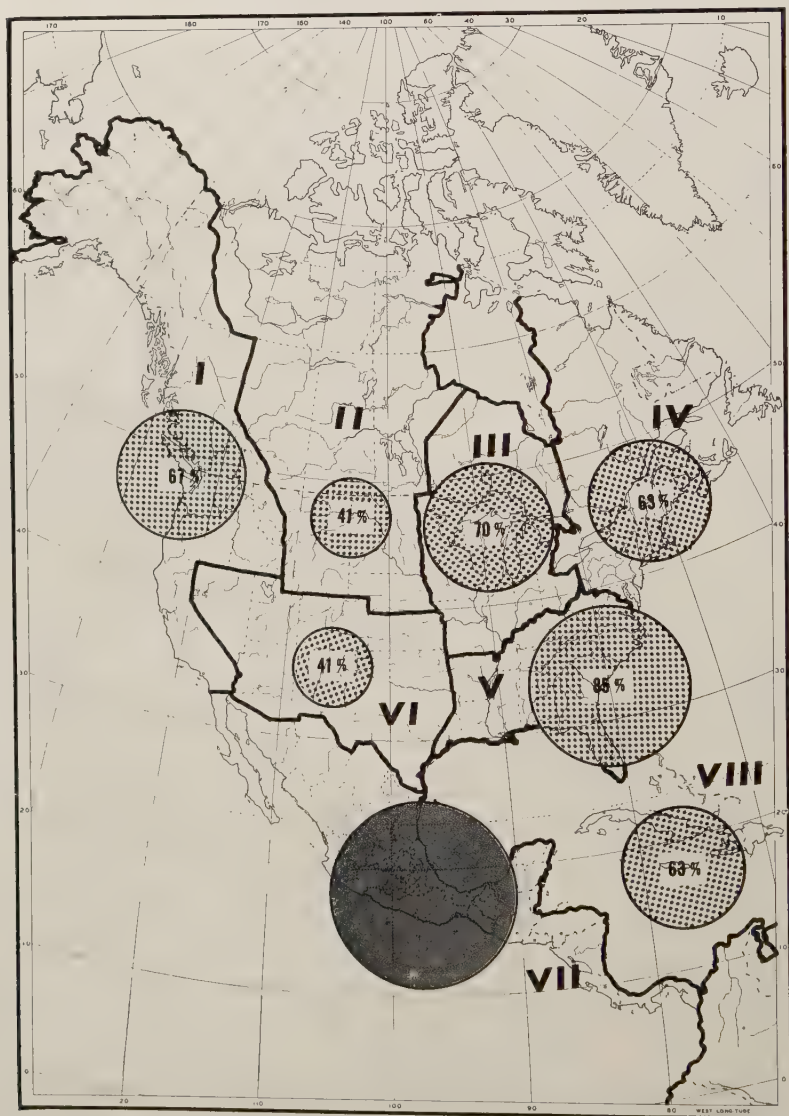


Fig. 1.—A comparison of the percentage of Mexican Thelephoraceae (dark circle representing 100%) found in the remaining regions of North America. Based on a collection of 27 Mexican thelephores, comparisons are valid only between Region VIII and the other regions.

in Region V might well be an independent region or subregion. However, for the present discussion and for reasons previously cited, it seems better to ignore such problems.

Region I includes Alaska (perhaps only the Pacific coast of Alaska belongs here), Yukon, British Columbia, Washington, Oregon, California, Idaho and western Montana. Region II consists of the Northwest Territories, Alberta, Saskatchewan, Manitoba, central and eastern Montana, North and South Dakota, Wyoming, and Nebraska. Region III includes Ontario (except the southeastern portion), Wisconsin, Minnesota, Michigan, Iowa, Missouri, Illinois, Indiana, and Ohio. Region IV includes southeastern Ontario, Quebec, Labrador, New Brunswick, Nova Scotia, and the New England and Middle Atlantic states. Region V is the southeastern United States from the Virginias, Kentucky, and Arkansas south to the Gulf of Mexico and west to eastern Texas. Region VI is formed by central and west Texas, west along the Mexican border to the Great Basin states and north to the northern borders of Kansas and Colorado. Region VII is Central America. Region VIII represents the West Indies (excluding Trinidad and its satellites as belonging floristically as well as physiographically to the South American mainland).

TABLE I.—Distribution of certain Mexican Thelephoraceae in North America

Species	Region							
	I	II	III	IV	V	VI	VII	VIII
1. <i>Aleurodiscus griseo-canis</i>			x					
2. <i>Coniophora olivacea</i>	x	x	x	x	x			
3. <i>Cora pavonia</i>					x		x	x
4. <i>Corticium lactescens</i>	x		x	x	x		x	x
5. <i>Corticium pelliculare</i>	x		x	x		x	x	x
6. <i>Corticium portentosum</i>	x		x	x	x		x	x
7. <i>Corticium sphaerosporum</i>				?	x			
8. <i>Cotylidia cyphelloides</i>								x
9. <i>Hymenochaete pinnatifida</i>					x		x	x
10. <i>Hymenochaete tabacina</i>	x	x	x	x	x	x	x	
11. <i>Pellicularia vaga</i>	x	x	x	x	x	x	x	
12. <i>Peniophora byssoides</i> subsp. <i>tomentella</i>					x		x	
13. <i>Peniophora cinerea</i>	x	x	x	x	x	x	x	x
14. <i>Peniophora roumeguerii</i>	x		x		x			x
15. <i>Peniophora tenuis</i>	x			x				x
16. <i>Phlebiella vaga</i>	x	x	x	x	x			x
17. <i>Stereum albobadium</i>	x	x	x	x	x	x	x	x
18. <i>Stereum crassum</i>	x		x	x	x	x	x	x
19. <i>Stereum complicatum</i>	x		x	x	x	x	x	x
20. <i>Stereum gausapatum</i>	x	x	x	x	x	x	x	x
21. <i>Stereum ochraceo-flavum</i>	x	x	x	x	x	x	x	x
22. <i>Stereum ostrea</i>					x		x	x
23. <i>Stereum papyrinum</i>							x	
24. <i>Stereum purpureum</i>	x	x	x	x	x		x	x
25. <i>Stereum sulphuratum</i>					x		x	
26. <i>Treichispora diademifera</i>	x	x	x	x	x	x	x	
27. <i>Xylobolus frustulatus</i>	x	x	x	x	x	x	x	

Tables I and II list the species we collected in Mexico and the regions in which they are reported to occur. Region VII should be considered to be completely filled, since this column represents the Mexican collections. However, those species for which we could find no previous report from Central America appear without checks in column VII. Table III records the percentages of species common in the various regions with our Mexican collections. Figures 1 and 2 are graphic representations of these percentages carried to the nearest whole number. Since these percentages are based only on Mexican collections, valid comparisons can only be made of Region VII with the other regions.

An inventory of Burt (1914-1926) and Murrill (1912) reveals that

TABLE II.—Distribution of certain Mexican Polyporaceae in North America

Species	Region							
	I	II	III	IV	V	VI	VII	VIII
1. <i>Bjerkandera adusta</i>	x	x	x	x	x	x	x	x
2. <i>Cerrenella ravenelii</i>					x			
3. <i>Coriolus abietinus</i>	x	x	x	x	x	x	x	x
4. <i>Coriolus maximus</i>					x		x	x
5. <i>Coriolus pinsitus</i>			x		x	x	x	x
6. <i>Coriolus sector</i>					x		x	x
7. <i>Coriolus versicolor</i>	x	x	x	x	x	x	x	x
8. <i>Cycloporellus iodinus</i>					x		x	x
9. <i>Daedalia elegans</i>			x		x	x	x	x
10. <i>Favolus rhipidium</i>			x	x	x			
11. <i>Fomes dependens</i>					x		x	x
12. <i>Fomes feei</i>					x		x	x
13. <i>Fomes geotropus</i>			x		x		x	x
14. <i>Fomes ohioensis</i>		x	x	x	x	x		x
15. <i>Fomes robiniae</i>	x		x	x	x	x	x	x
16. <i>Fomes roseus</i>	x	x		x		x	x	x
17. <i>Ganoderma lobatum</i>			x	x	x	x		
18. <i>Ganoderma lucidum</i>	x	x	x	x	x			
19. <i>Gloeophyllum sepiaria</i>	x	x	x	x	x	x	x	x
20. <i>Hapalopilus gilvus</i>	x	x	x	x	x	x	x	x
21. <i>Hapalopilus lichnoides</i>					x		x	x
22. <i>Hexagona tenuis</i>							x	x
23. <i>Irpex lacteus</i>	x	x	x	x	x	x	x	x
24. <i>Pogonomyces hydroides</i>					x		x	x
25. <i>Polyporus arcularis</i>		x	x	x	x	x	x	x
26. <i>Polyporus biennis</i>	x	x	x	x	x			x
27. <i>Polyporus dichrous</i>	x	x	x	x	x	x		
28. <i>Polyporus occidentalis</i>								
29. <i>Polyporus zonalis</i>					x		x	x
30. <i>Poria regularis</i>					x			x
31. <i>Poria taxicola</i>	x	x	x	x	x	x		
32. <i>Poria tenuis</i>	x	x	x	x	x	x		
33. <i>Pycnoporus sanguineus</i>		x	x	x	x	x	x	x
34. <i>Trametes rigida</i>			x	x	x		x	x
35. <i>Trametes sepium</i>	x	x	x	x	x	x	x	x

the sixty-two species considered here represent a substantial percentage of the known Mexican thelephores and polypores. Wherever possible, synonyms have been taken into account using the works of Boidin (1958; 1959a, b), Lowe (1957), Overholts (1953), Rogers and Jack-

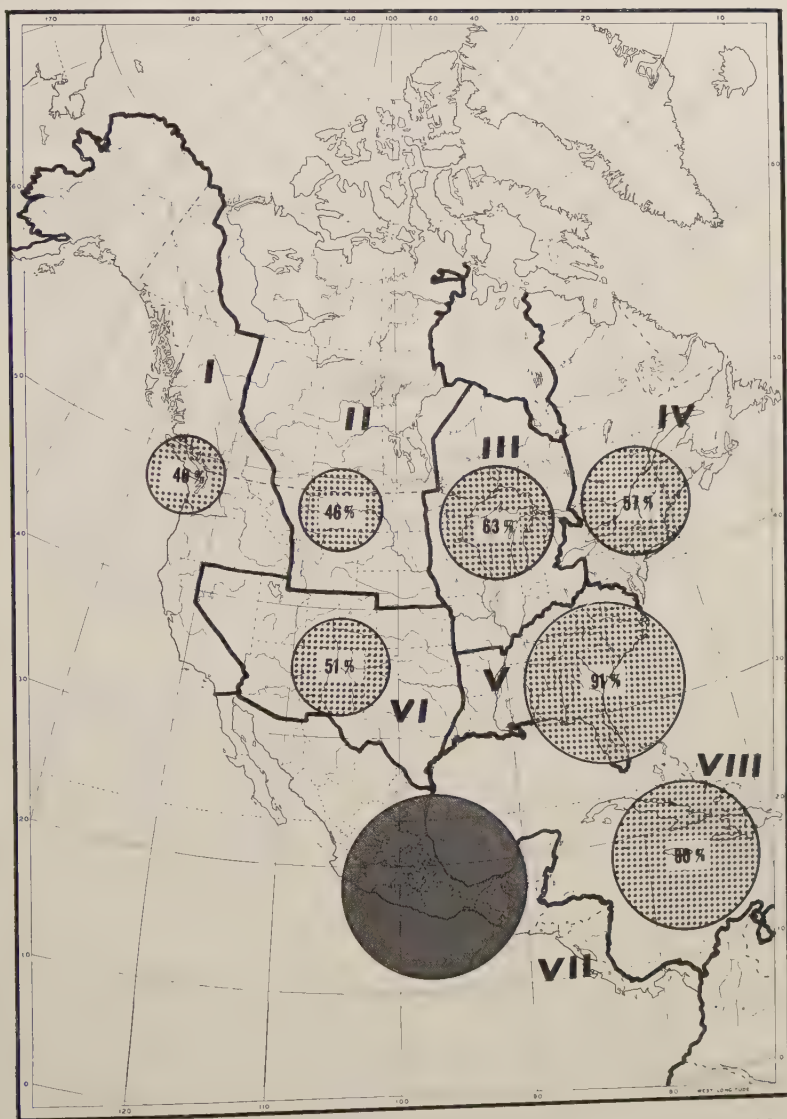


Fig. 2.—A comparison of the percentage of Mexican Polyporaceae (dark circle representing 100%) found in the remaining regions of North America. Based on a collection of 35 Mexican polypores, comparisons are valid only between Region VII and the other regions.

TABLE III.—Percentage of Mexican species represented in other regions of North America

Region	Thelephoraceae	Polyporaceae	Thelephoraceae and Polyporaceae
I	66.6	40.0	51.6
II	40.7	45.7	43.5
III	70.3	62.9	66.1
IV	62.9	57.1	54.8
V	85.2	91.4	88.7
VI	40.7	51.4	46.7
VIII	62.9	80.0	72.6

son (1943), and others. Accordingly, Burt lists seventy-two species from Mexico; to which we now add thirteen species not previously reported, bringing the total number to eighty-five species. Murrill gives one-hundred and eighteen species (twenty-four considered by him to be new to science); to which we add thirteen unreported by him, bringing the total number to one-hundred and thirty-one species. Therefore, our collection of twenty-seven thelephores and thirty-five polypores represents about 32 per cent of the known Mexican Thelephoraceae and 27 per cent of the Polyporaceae.

The most striking feature, in considering the Thelephoraceae (Fig. 1, Table III), is the high degree of identical species in Mexico and the southeastern United States. Sharp (1948) has shown a similar finding between the Mexican and Guatemalan highlands' fungi and the Appalachian fungi, using a number of species widely scattered in different taxonomic categories. Our collections were made from lowlands as well as highlands. Perhaps, this similarity could be enhanced by dividing the Mexican fungi into highland and lowland species and comparing them with the Gulf coastal plains and Appalachian species. The next highest degree of similarity is shown by comparing Region VIII and Region III. The Mississippi River basin appears to afford a favorable habitat for the thelephoraceous fungi which are also found in tropical and subtropical North America. Oddly enough, Pacific North America demonstrates a higher degree of similarity with Mexican Thelephoraceae than does the West Indies. This difference is not high and may be shown in the future to be caused by the lack of collecting in the Antilles. Regions II and VI show the poorest correlation. The lack of suitable substrates and abundant water may account for this. Finally, Region IV has a higher degree of similarity than Regions II and VI.

As in the Thelephoraceae, the Polyporaceae (Fig. 2, Table III) show the same correlation between Regions VII and V, with an even higher percentage of similitude. Region VIII, however, closely approaches Region V and here outranks Region III. The polypores are relatively well collected and this shift would not seem to be caused by better collecting in one area than another. This may well portend a similar shift in the thelephores as they become better known in Region

VIII. The relative paucity of polyporaceous species in common between Region VII and Region I, and the greater number represented in Regions II and VI is noteworthy. The Thelephoraceae seem to suggest the reverse with a larger percentage occurring in Region I. This difference cannot at present be explained. Once again, substrate relations might be considered.

Column 3 of Table III compiles the percentages of both Mexican thelephores and polypores as represented within the remaining regions. In decreasing order of similarity the Regions are V, VIII, IV, I, and II. Treating the families combined, however, is not as informative as keeping them separate. Indeed, comparisons at the generic level should prove to be even more interesting. It is also obvious that a world-wide comparison would be enlightening, but the lack of data at present makes this extremely difficult.

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Vocalization as an Isolating Mechanism in Frogs

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ABSTRACT: In laboratory tests, female *Hyla crucifer* selected the call of their own species in preference to that of *Pseudacris triseriata*, but not in preference to that of *P. ornata*.

Female *triseriata* selected the call of their own species instead of that of the allopatric leptodactylid *Eleutherodactylus portoricensis*. On the other hand, only about 8 out of 10 succeeded when given a chance to respond to the calls of sympatric hylids—*P. ornata*, *P. brachyphona* and *H. crucifer*. Local *P. triseriata* females were unable to discriminate between a call of a member of their own population and that of a frog recorded in New York; however, when given a chance to respond to a call recorded in Manitoba, 8 out of 9 reacted to the locally recorded call.

Thus, for some species, vocalization is a major isolating mechanism, for others it is partially effective, and for still others it is ineffective. In those species in which vocalization is not a complete isolating mechanism, other factors—such as body size, rather small and subtle differences in behavior, habitat preference and timing—prevent interspecific matings.

As is well known, optimum conditions for amphibian reproduction are generally associated with rainfall. At such times, numerous individuals of several species often aggregate in the same pond. In these situations, it is important that interspecific matings be avoided. The latter result in gross biological inefficiency. Special secretions produced by the hedonic glands of males contribute greatly in preventing interspecific matings from occurring among most caudate amphibians. Among the Anura, such glands are absent. Numerous workers (Noble, 1931; A. P. Blair, 1941a, 1942; W. F. Blair, 1955, 1956; and many others) have stated that the calls of anurans serve to prevent crossing of the various species utilizing the same breeding site. However, there are no experimental data to verify this conclusion. With the recent observations that *Pseudacris triseriata* undergoes reproductive behavior in the laboratory and that the mating call alone guides a female to a particular male (Martof and Thompson, 1958), a method was provided for the testing of frog calls as an isolating mechanism.

Acknowledgments.—This study was supported by the National Science Foundation. I am grateful to Paul Kellogg (Cornell University Library of Natural Sounds) for the use of recordings of *Pseudacris triseriata* made in New York and in Manitoba and for the recording of *P. ornata*. I am especially indebted to Eric F. Thompson, Jr. for the recording of *Eleutherodactylus*, for the preparation of the recorded calls used in this study, and for assistance with the tests.

METHODS

From field-made recordings of various frogs (mostly sympatric hylids), single calls having a minimum of background noise were selected. Each call was transferred to a loop of tape constructed so that

the call was repeated at approximately its natural rate. In each test conducted, two such loops were simultaneously played back via the same type of recorders (Magnetic model Nos. P63 and P73) and and speakers (Mytron crystal earphones, model No. N-98). The speakers were placed at opposite ends of a 5' x 8' x 4" indoor tank, provided with numerous scattered clumps of sedges and grasses and with water having a uniform depth of about 0.75". A 21-inch strip of burlap, supported by stakes placed every two feet around the tank, prevented frogs from jumping out of the tank. Furthermore, the burlap was an effective "screen" behind which observers could move without disturbing the frogs in the tank. Calls were played back with about the same relative loudness that they occur in nature. The more similar calls, those of various populations of *Pseudacris triseriata*, were adjusted by balancing the voltages across the speakers so that the intensity of each call was the same. After a few frogs were tested, the calls were shifted from one speaker to the other. Thus any bias in the tank or in the play-back systems tended to cancel out. This was done routinely even though such bias appeared to be absent.

Locally captured gravid females of *Hyla crucifer* and *Pseudacris triseriata* were used in this study. These are the only hylids which occur in Clarke County, Georgia and which breed in February and March. Practically all specimens were captured along highways near breeding areas. Only a few frogs were collected in the breeding areas. All specimens used in the laboratory were not in amplexus when captured. These animals were kept in a refrigerator at 6° C. and were used within a few days after capture. About an hour before the frogs were to be tested, they were placed in a sound-proof box where the temperature was the same as that in the laboratory (18-20° C.). The laboratory was evenly lighted by overhead fluorescent lights, dimmed during the tests. Each female was used once and at most, only two specimens were in the tank at the same time. The frogs to be tested were placed in a small screen enclosure located along one side of the tank midway between the speakers. Here they were retained for about 15 seconds — long enough to recover from handling, yet not long enough to evoke escape behavior due to confinement. Each female was observed closely and her path and behavior noted.

Upon release into the tank, most females remained motionless for several minutes. However, above a third of them went first into a nearby clump of vegetation before becoming quiescent. Only a few females reacted to a call immediately upon being released. Usually the first outward indication that a female was going to react was that she turned her head (often her entire body) and faced one of the speakers. Some frogs oriented toward one speaker and then toward the other — apparently they had some difficulty in making a choice. However, once a female began to show interest in the calls, a reaction soon followed. Usually she hopped directly

to a speaker and often upon it. When within a few inches in front of, or under, or on the speaker, she generally remained there 30 seconds to about 12 minutes. After responding to one call, some females responded to the call arising from the other speaker. This situation was further complicated because sometimes the second response was more intense than the first. Because of this type of behavior, two criteria were established as being prerequisite to a "reaction."

I. The frog had to move directly to a speaker and at the same time provide overt evidence that she was attentive to the call produced there. The latter consisted of (a) her facing the speaker, usually with head high and alert, and in the meantime (b) the absence of escape behavior (erratic hopping and much climbing onto the burlap around the tank). In every instance, there had to be no doubt that the frog got to a speaker by deliberate movements rather than by accidental wandering.

II. The second requirement for a "reaction" was that, had a male been present in place of the speaker, amplexus would have resulted as a consequence of the female's behavior. For each frog, only the first response which met these requirements was counted.

Depending on the amount and kind of activity shown by a female, an experiment was terminated if no reaction occurred within 30 to 60 minutes. Those females which did not respond to either call spent practically all their time in the vegetation where they remained quiescent or else they slowly climbed up the vegetation and eventually onto the burlap. Such behavior was identical to that of frogs not subjected to any calls. Accordingly, the number of these "non-reactions" was not considered in the determination of the probability associated with each set of experiments. Generally each series of tests included about ten reactions. The probability that the results (the ratio of the number of frogs which reacted to each call) were due solely to chance was determined by the Chi-square method.

RESULTS

Hyla crucifer

The results obtained for *Hyla crucifer* are more explicit than those for *P. triseriata*. The females reacted to the call of the male in a manner very similar to that described for *triseriata* (Martof and Thompson, 1958); however, the following differences were noted. The female *crucifer* spent more time on and in the vegetation, they hopped more, and climbed onto the speaker more. Furthermore, their average reaction time was 15.8 minutes which is shorter than that of *triseriata* (18.2 minutes). In both species about 88 per cent of the time spent in the tank involved a long pause which occurred immediately after a frog was released. Once a frog started to react, she usually went promptly to a speaker. There was one other way in which the behavior of *crucifer* was outstanding. After moving to a speaker, about a third of the females repeatedly jumped against the side of the tank near the speaker. They would hit into the tank wall

about three inches from the bottom and fall back into the water, often with venter up. One female did this 25 times within four minutes. This obviously was not escape behavior. *Hyla crucifer* is a graceful, agile hopper and climber, in sharp contrast these actions were definitely awkward, clumsylike. In *Pseudacris*, sex recognition usually involves the female's crawling into contact with the antero-ventral part of the calling male, whereas in *Hyla* the female usually jumps onto the male. Thus, the jumping against the side of the tank by the female *crucifer* very likely was a misdirected attempt to get to the sound source. This difficulty in localizing the sound was probably due to inherent qualities of the earphones used as speakers. Furthermore, male *crucifer* generally call from on vegetation a few inches to a few feet from the water; whereas, male *triseriata* call usually from in the water.

The call of *crucifer* is a short, clear, high-pitched whistle consisting of a single note with an upward slur at its end. This call has an average dominant frequency of 3200 cycles per second (cps) and a duration of 0.13 sec.; it is repeated about once per second. On the other hand, the call of local *triseriata* consists of a series of varied notes given in rapid succession so as to produce a penetrating, grating sound, often likened to that made by passing the thumb over the teeth of a comb. On the average, this pulsed call consists of 17 notes having a dominant frequency of about 2700 cps and a duration of 0.75 sec. It is repeated about every 2.5 sec.

All female *crucifer* used in 1959 were captured on March 11th. The next day some of them were given a choice of reacting to the call of their own species and to that of *triseriata*. Nine reacted to the call of *crucifer* and none to that of *triseriata* (Table I). The probability that such results would occur by chance alone is very slight

TABLE I.—The response of gravid female *Hyla crucifer* to a choice between a call of their own species and one of another species

Alternative	Number of females reacting to call of <i>crucifer</i> - alternative	Probability (Chi-square)	Efficiency of isolation (estimated)
<i>Pseudacris triseriata</i> (Athens, Ga.)			
Mar. 12, '59	9 - 0		
Feb. 24, '60	14 - 1		
total	23 - 1	.001	92%
<i>Pseudacris ornata</i> (Gainesville, Fla.)			
Mar. 12 & 15, '59	10 - 11		
Feb. 29, 1960	13 - 7		
total	23 - 18	.60	8%

(0.03). Obviously, female *crucifer* are effectively isolated from male *triseriata*.

On the same night, some *crucifer* females were subjected to the call of their own species and to that of *Pseudacris ornata*. The call of *ornata* consists of a single note which is also loud and distinctive; however, it is only about one-fourth as long as that of *crucifer* and is repeated about twice as frequently. It has an average dominant frequency of 2800 cps and is more metallic in quality (suggesting the sound made by a hammer squarely hitting a chisel).

In sharp contrast to the results obtained with the *triseriata* call, the female *crucifer* showed no preference for the call of their own species over that of *ornata*. Three females selected the call of *crucifer* while four responded to that of *ornata*. Three days later, more females were tested. At this date, seven females reacted to each call making a total of 10 reactions to the call of *crucifer* and 11 to that of *ornata*. The probability that selection of the call was due to chance alone is very high. Accordingly these data strongly suggest that the frogs were unable to discriminate between the calls offered. This is of great biological importance because about 90 per cent of the geographic range of *ornata* is also occupied by *crucifer*.

In 1960 additional observations were made. On February 24th, *crucifer* females captured in the field only a few hours previously were subjected to *crucifer* and *triseriata* calls. Fourteen of the 15 which reacted went to the call of their own species. The single reaction to the *triseriata* call was in every way similar to those made to the call of *crucifer*. Moreover, the frog involved was morphologi-

TABLE II.—The response of female *Pseudacris triseriata* to a choice between a call of the same population and one of another population

Alternative	Number of females reacting to call of <i>triseriata</i> - alternative	Probability (Chi-square)	Estimated Efficiency of isolation
<i>P. triseriata</i> (Rochester, N. Y.)			
Feb. 26, '59	5 - 5	1.00	0%
<i>P. triseriata</i> (Ft. Churchill, Man.)			
Feb. 24, '59	8 - 1	.10	78%
<i>P. brachyphona</i> (Amicolola Falls, Ga.)			
Feb. 27, '59	9 - 3	.22	50%
<i>P. ornata</i> (Gainesville, Fla.)			
Mar. 1, '59	8 - 2	.20	60%
<i>Hyla crucifer</i> (Athens, Ga.)			
Mar. 14, '59	8 - 2		
Feb. 10, '60	7 - 2		
total	15 - 4	.08	58%
<i>Eleutherodactylus</i> sp. (Puerto Rico)			
Feb. 28, '59	3 - 0	.22	100%

cally a *crucifer*. This is significant because hybrids of these two species have been produced in the laboratory (Blair, 1941b, Gosner, 1956). The over-all performance of 23 reactions to the call of their own species and only one to that of *triseriata* indicates that a high degree of isolation is afforded by vocalization.

On February 29th, freshly captured *crucifer* were tested against the call of *ornata*. Thirteen of the 20 reactions were to the call of *crucifer*. These results are in general consistent with those obtained in 1959 and indicate a relatively low degree of vocal isolation.

Pseudacris triseriata

Between February 24 and March 14, 1959, 54 female *triseriata* reacted to a choice between the call of a local *triseriata* and that of another population. Calls from specimens recorded in New York and Manitoba closely approximate that of local specimens (Thompson and Martof, 1957). However, the Manitoba call has the highest dominant frequency (3100 cps) and the shortest duration (0.58 sec.). These characteristics make it less melodic and more tinny in quality. On the other hand, the call of *triseriata* from New York is very similar to that of local frogs in average dominant frequency (2600 cps) but is more like the Manitoba call in duration (0.60 sec.). The call of the New York population has 20 notes, that from Manitoba 18 notes.

In this series of tests, a surprisingly large number (five out of ten) of the local females was attracted to the New York call. In sharp contrast, only one female out of nine preferred the Manitoba call to that of the local population. The latter results are significant at the ten per cent level of probability and possibly indicate some isolation.

The calls produced by other species of *Pseudacris* (*brachyphona* and *ornata*) were also tested. Because of its nasal quality the call of *brachyphona* is easily distinguished (by humans) from those of the various populations of *triseriata*. Its call is of shorter duration (0.46 sec.), has a lower average dominant frequency (2250 cps), and contains many more notes (about 25). Three of the twelve female *triseriata* tested, selected the call of *brachyphona* to that of *triseriata*. The probability that these results were due to chance alone is 0.22.

Even though the call of *ornata* is very different from that of *triseriata*, two of the ten female *triseriata* tested, preferred it to that of their own species. These results are significant at the six per cent level of probability.

As described earlier, the call of *ornata* is similar in many of its parameters to that of *crucifer*; furthermore, female *crucifer* reacted equally well to the call of *ornata* and to that of their own species. Accordingly, it is of special interest to note that two out of ten *triseriata* selected the call of *crucifer* to that of *triseriata*. This is the same ratio as was obtained when the call of *ornata* was used.

In contrast to the previous experiments with sympatric and closely related forms, the call of the allopatric, *Eleutherodactylus portoricensis* was used. The common name of this frog, "co-qui," very adequately describes its call which consists of two distinct notes of equal duration (0.091 sec.). These notes are separated by a relatively long interval (0.137 sec.) and differ greatly in their average dominant frequencies, 900 and 2050 cps, respectively. When three female *triseriata* were given a choice between this call and that of their own population, they reacted to the latter. In as much as they showed no interest in the call of *Eleutherodactylus*, additional specimens were not tested.

In 1960 *triseriata* were again tested with a call of a local *triseriata* and one of *crucifer*. Seven of the nine females which reacted went to the call of their own species. These data are in accord with those obtained in 1959.

DISCUSSION

It is recognized that the absence of a background chorus of calling frogs produced a somewhat artificial setting for the testing of frogs; however, in a study of a complex stimulus, such as the mating call, it is highly desirable to isolate the call so that it can be subjected to more careful scrutiny. Moreover, the results obtained indicate that background calls are not essential to the reaction of the female; however, had they been present, it is possible that the frogs would have reacted more quickly. Other artificialities included changes in the acoustic properties of the environment, differences in lighting, small changes incidental to recording and playback of calls, etc. Temperature differences were also involved. For example, the call of local *triseriata* was recorded at a temperature of 15.0° C. (water), *crucifer* at 17.8° (air), *Eleutherodactylus* at 29.4° (air), and *brachyphona* at 8.9° (water). For the other calls, temperature data were not available. Also lacking were details on recording conditions, such as location of microphone with regard to the calling frog. In spite of the absence of these desiderata, the general characteristics of the calls of each species are contained rather accurately in the test calls.

Why all frogs did not react is difficult to determine. Many factors are here involved: mainly, individual differences in their internal state of readiness for reproduction and secondly, differences in their adjustment to handling and to laboratory conditions. Also to be mentioned, is the possible effect of refrigeration. Table III contains a list of the number of frogs that did not react in each series of tests and also the duration of the periods of refrigeration. No clear-cut relationship is evident. In 1960 the *triseriata* were dissected immediately upon being tested. It is highly pertinent that the eggs of the nine females that reacted were in the ovisacs while those of the three that did not react were still in the ovaries. These data strongly suggest that ovulation is prerequisite to mating for this species.

Because of the relatively small number of animals used in this study, the results for each set of tests provide only a general approxi-

mation of the degree of isolation afforded by vocalization. The general efficiency of each set of calls was determined in the following way. If as many females went to one call as went to the alternative, the efficiency was interpreted to be 0 per cent. Likewise, if all females reacted to the call of their own species, the efficiency was 100 per cent. Accordingly, if three out of ten went to the alternative call, the efficiency was only 40 per cent. The efficiency of the various sets of calls is provided in Tables I and II. For some groups, such as female *crucifer* and male *triseriata*, vocalization is a highly effective isolating mechanism. In contrast, female *triseriata* are not completely isolated by vocalization from any of the other hylids tested.

The amount of isolation between two species is not completely dependent upon the amount of structural differentiation exhibited in their calls. This is clearly indicated by the fact that *triseriata* females responded to most calls made available to them. These calls varied considerably in complexity, yet about the same proportion of females reacted to each (see Table II). Structural differentiation of calls may produce isolation but some major physical changes seemingly do not alter the isolative powers of calls.

It is imperative that the differential effectiveness of calls be considered for all species wherein reproductive isolation is studied. For example, four out of 19 female *triseriata* responded to the call of *crucifer*; however, only one out of 24 female *crucifer* responded to the call of *triseriata*. Because of the greater efficacy of vocalization in the reciprocal mating, the efficiency of isolation between these species is not 58 per cent (as given in Table II) but more accurately is 75 per cent. Because reciprocal tests for the other groups are not currently available, the data in Tables I and II are based on unilateral experiments.

TABLE III.—The temporal distribution of "non-reactions" and their relationship to refrigeration

Date	Days under refrigeration	Number of Reactions - Non-reactions	Percent which did not react
<i>Hyla crucifer</i>			
Mar. 12, '59	1	16 - 2	11
Mar. 15, '59	4	14 - 4	22
Feb. 24, '60	0	15 - 2	12
Feb. 29, '60	0	20 - 3	13
<i>Pseudacris triseriata</i>			
Feb. 24, '59	10	9 - 2	18
Feb. 26, '59	0	10 - 4	29
Feb. 27, '59	1	12 - 2	14
Feb. 28, '59	2	3 - 0	0
Mar. 1, '59	3	10 - 2	17
Mar. 14, '59	3	10 - 1	9
Feb. 10, '60	0	9 - 3	25

Another factor which must be considered, if reproduction isolation is to be evaluated precisely, is the relative sizes of the populations occupying a particular breeding area. This is especially applicable to local *crucifer* and *triseriata*. The main part of the *triseriata* population breeds somewhat earlier in the season than does the main part of the *crucifer* population. As a consequence, *crucifer* males are relatively scarce during the peak of the *triseriata* breeding season and *triseriata* males are less abundant during the peak of the *crucifer* season. There is yet another factor which is pertinent. The calling *triseriata* males are usually more closely aggregated than are those of *crucifer*, even during the peak of the latter's breeding season. Thus interspecific matings between these sympatric forms are greatly inhibited by many factors, none of which is completely successful when operating alone.

It is noteworthy that *triseriata* having a relatively elaborate call, is not completely isolated from most related species — those with equally elaborate calls as well as those with simpler calls. In contrast, *crucifer* has a relatively simple call and is effectively isolated from *triseriata* (and very probably from others with similar calls) but not from *ornata*, which also has a simple call.

This study provides a method wherein the effectiveness of vocalization as an isolating mechanism can be accurately measured for many species. However, what is critically needed to promote understanding of the role of vocalization is knowledge of (1) those parameters of a call which elicit a reaction from a female frog, and (2) the hearing ability of frogs.

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Observations of the Activities of Small Animals (Reptilia and Mammalia) on a Quadrat in Southwest Texas

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ABSTRACT: Observations on the daily activities of reptiles and small mammals were made on a quadrat near Alpine, Brewster County, Texas, during the early summer of 1957. Thirty-six live-mouse traps and nine nest boxes were arranged in grid patterns on a quadrat 300 feet square. Thirteen drift-fence traps were arranged in two lines which bisected the quadrat in north-south and east-west directions, and crossed in the center of the quadrat.

During the study 114 reptiles of nine species, mostly lizards, were marked and released, and 74 of these were recovered at least once for a total of 230 recoveries. Whiptail lizards (*Cnemidophorus sacki*) formed the bulk of the reptiles captured and recovered. Nineteen mammals of three species were marked and released, and seven were recovered for a total of 22 recoveries. On the basis of the observed activities of other animals reported in various papers, it is proposed that the term "home realm" be adopted for all of the area in which an animal is normally active. The term "home range" then becomes restricted to the smaller, inner area in which an animal is usually active.

In recent years, there have been a number of investigations of the population dynamics of reptiles and mammals in southwestern Texas. York (1949) studied the movements of mice in the Sierra Vieja range of Presidio county, and Anderson (1949) recorded the activities of mule deer in the same area. Louis Follansbee (1951, unpublished) and Dixon (1958) studied the movements of mice on the Black Gap Wildlife Management Area of Brewster county. Milstead (1957 a,b,; 1959; In press) compared the activities of *Cnemidophorus* and other lizards at Black Gap and other stations, and W. G. Degenhardt is currently completing an investigation of the movements of various reptiles in Big Bend National Park. The present report is concerned with another study of population dynamics of small vertebrates in southwest Texas, but this work differs from the others in that it was the first attempt to study reptiles and mammals simultaneously on the same quadrat. In effect, it was an attempt to study the movements of all small vertebrates exclusive of birds. The purpose of this paper is to report on the methods used, the effectiveness of those methods, and the observations made.

The study area is located on the Sul Ross State College Ranch, one mile east of Alpine, Brewster County, Texas. The work was done by a Sul Ross field zoology class under the direction of the writer from June 6 to July 9, 1957.

Acknowledgments.—Thanks are due the members of the Department of Range Animal Husbandry for permission to carry out this study on land in their

charge. I am indebted to Dr. Barton H. Warnock of the Sul Ross Biology Department for information on the vegetation of the region. Special credit is due the fourteen field zoology students who in their study of ecology in the field made the bulk of the observations here reported. Especial thanks are accorded Mr. Reece DeGraffenried for his aid in preparation for the course.

STUDY AREA

The Sul Ross State College Ranch lies in the eastern portion of the Davis Mountains biotic district of Blair (1940, 1950) and Milstead (In press). The study area exhibits no outstanding faunistic or floristic differences from the interior of the district. The Davis Mountains are in the Chihuahuan biotic province of Blair (1940, 1950) and Dice (1943), and in the Basin and Ranges physiographic province of King (1937). The quadrat was located in the Short-Grass—Mesquite association of Blair (1940). The dominant vegetation of the quadrat consists of low mesquite (*Prosopis juliflora*), mesquit (*Acacia constricta*), lote bush (*Condalia lycioides*), tasajillo (*Opuntia leptocaulis*), prickly pear (*Opuntia* sp.) yucca (*Yucca torreyi* and *Y. elata*), and local stands of grasses, tobosa (*Hilaria mutica*), blue grama (*Bouteloua gracilis*), and black grama (*Bouteloua eriopoda*). The average elevation of the quadrat area is about 4600 feet. Except for a slight rise in the northwest corner and a slight, over-all dip to the east, the site of the quadrat is fairly level. Drainage is into a small draw located about 50 yards to the east of the study area.

METHODS

The quadrat was 300 feet square and three types of traps were employed on it: 36 live-mouse traps built according to the specifications given by Blair (1941), nine nest-box traps similar to those used by Howard (1949), and 13 drift-fence traps of the type used by Milstead (1957b, 1959). The live-mouse traps were arranged in a grid pattern with approximately 60 feet separating the traps. The distances between the traps were not always exactly 60 feet, but varied as much as 10 feet from this figure in order to better utilize available natural cover. The outer lines of the live-mouse traps formed the boundaries of the quadrat. The nest boxes were arranged in a smaller grid within the mouse trap grid. The nest boxes were separated by approximately 125 feet, and distances of approximately 40 feet separated the boxes and the mouse traps. The drift-fence traps were spaced 50 feet apart and were connected by 12-inch-high drift fences. The traps and fences were arranged in the pattern of a cross with one line bisecting the quadrat from north to south and the other from east to west. The center trap where the two lines crossed was constructed in the shape of a cross with an entrance facing each direction. The approximate positions of all of the traps and fences are shown in Figure 1.

During the first few days of the study and on the last day, all of the students and the writer were present on the quadrat. For most of the

study, however, no more than eight people were on the quadrat at any one time.

The 36 live-mouse traps were baited on all but three nights of the study for a total of 1,008 trap nights. The bait consisted of a mixture of rolled oats and peanut butter. Although both the traps and the bait had been used previously in the same area with success, there were few captures and recoveries during this study. Simultaneous use of this type of trap and bait by the same workers at various other localities throughout the Davis Mountains also yielded poor returns. This suggests that the poor results may have been due to low rodent population density during the summer of 1957. The traps on the quadrat were closed during the daytime to prevent lizards from entering, tripping the trigger, and then perishing from the heat which accumulates in the traps during the day. The closure of the traps also prevented the entrance of ground squirrels (*Citellus*) and other diurnal animals. This was the only outstanding disadvantage of working with reptiles and mammals simultaneously.

The nest boxes were buried in the ground with only the lids and entrances protruding. They were not baited, but were provided with newspapers for nesting material. During the study, only one animal, a lizard (*Cnemidophorus sacki*) was found in a nest box. Although the boxes were left in the ground and periodically checked until late November, no small animal ever used them for a nesting site. The apparent low rodent density in 1957 may explain the failure of these traps. Workers in other parts of Texas (Blair, 1958; Blair and Kennerly, 1959; McCarley, 1958), however, have reported that rodents are reluctant to use nest boxes during the summer months. The boxes on the quadrat were eventually rendered useless by influx of silt and debris during floods created by fall rains. During use of nest boxes in overgrazed, arid regions, where rapid water run-off occurs, it is suggested that the entrances to the boxes project at least two inches above ground.

The drift-fence traps were operated with dirt-covered entrances, with overhanging shades, and without trapdoors, as described by Milstead (1957b, 1959). The traps were not baited, although trapped animals may have served to some extent as bait for other animals. For the most part, however, captures were the result of animals having been guided into the traps by the drift fences. The traps and fences were kept in continuous operation for the first week of the study and proved to be highly effective with lizards. After the first week, the number of captures and recoveries showed a marked decline. Apparently, the effectiveness of the traps and the number (15) of people on the quadrat during the first few days of the study caused the lizards to avoid the traps and fences. The traps were removed on the eighth day of the study. They were replaced on the 12th day and the number of captures and recoveries showed a slight increase for the next few days. For the remainder of the study, the traps were kept in operation for only four consecutive days of each week. In spite of these difficul-

ties, the number of captures and recoveries indicates that this crossed-lines method of drift-fence trap operation is better than the standard single-line method. It is suggested for future studies, however, that better data may be obtained if the traps are used on alternate days or kept in operation for no more than two consecutive days. In addition to lizards, two snakes (*Masticophis* and *Hypsiglena*), two pocket mice (*Perognathus*), and various invertebrates were captured in the drift-fence traps.

After capture, mice and lizards were permanently marked by toe clipping. The toes were so numbered that no more than one toe was removed from any one foot. One snake was marked by clipped subcaudal scales, and a turtle by a notch cut in the first marginal scute. Two jackrabbits were marked with ear notches. In addition to permanent marking, lizards were temporarily marked with a bright lacquer which permitted easy recognition until ecdysis or abrasion removed the lacquer (see Milstead, 1959, for a discussion of this marking method). Recoveries of these lizards and other animals outside of traps were recorded in number of paces to the nearest trap or nest box.

WEATHER AND ANIMAL ACTIVITY

A weather station was maintained in the center of the quadrat throughout the study. The instruments included a maximum-minimum thermometer for air temperatures, a modified Mason's form hygrometer, a portable anemometer with a recording needle for maximum wind gusts, and a clear-bulb thermometer for reading soil temperatures. The maximum-minimum thermometer and the hygrometer were mounted in a weather box four feet above the ground and the anemometer was attached to the exterior of the box. Soil temperature was taken with the full length of the thermometer bulb stuck into the soil and the remainder of the thermometer shaded from direct sunlight. The Mason's form hygrometer was modified by the substitution of a wet-bulb, Schultheis museum thermometer for the standard wet-bulb thermometer. This permitted more rapid readings, and readings that compared more favorably with a sling psychrometer.

The average minimum air temperature during the study was 18.5° C., and the average maximum was 34.4° C. The lowest temperature recorded was 13.0° C. on June 20, and the highest was 41.0° C. on June 28. The highest soil temperature recorded was 55° C. on several days at intervals throughout the study. The highest wind velocity recorded was 40 km/hr on the morning of June 11 before lizard activity began. The highest recorded during lizard activity was 30 km/hr. Wind appeared to have little influence on the trapping of mammals or on reptile activity. No sustained winds of high velocity were recorded during the study, however. Use of the anemometer was discontinued after the second week upon failure of a bearing. Rain fell on four occasions during the study, but amounted to less than half an inch each time. Each rain was a cloudburst of short duration.

In Table I, averages of relative humidity and soil and air tempera-

tures are given for each hour of the morning, and the total numbers of reptile records are given for each half hour. Time is used here as the only available standard for comparison. The relative humidity and temperatures of any given moment are dependent upon a number of factors, but they do show a diurnal trend. This trend is evidenced by comparing the hourly averages. Reptile activity follows the same trend as the relative humidity and soil and air temperatures, but is most closely correlated with soil temperature (Table I and Milstead 1957b, 1959). The average temperatures of the Alpine area are considerably lower than those given by Milstead (1959) for the Black Gap area in southern Brewster county. This is attributed to differences in elevation. The Alpine area is approximately 2,000 feet higher than Black Gap. As a possible response to the lower temperature of Alpine, the lizards have a maximum activity period of about half that of Black Gap lizards: 9:00 to 10:30 AM at Alpine and 8:00 to 11:00 AM at Black Gap. For the most part, however, the species and subspecies differ at the two areas, and this may be the reason for the activity differences.

Most of the mammal captures were in traps. The traps were checked at approximately the same time each morning, and there is no way of determining at what hour or temperature a trap was entered. Of a total of 39 captures of *Perognathus hispidus* and *Dipodomys merriami*, 26 were made during the seven days from June 25 to July 1. These were the hottest days and nights of the study, but also the time during which the moon was in its darkest phases.

HOME RANGE, TERRITORY AND HOME REALM

Many terms have been used to describe the areas within which animals move about as they carry out the normal functions of their lives. Only two terms, however, "home range" and "territory," have

TABLE I.—Correlation of total reptile records, average soil and air temperatures, and average relative humidity with morning time intervals (see text for further explanation).

Species	Time							
	0800	0830	0900	0930	1000	1030	1100	1130
<i>Terrapene ornata</i>	1							
<i>Holbrookia maculata</i>	4	9	7	9	8	7	2	
<i>Sceloporus undulatus</i>	4	3	2	3	2	3	1	
<i>Phrynosoma modestum</i>	1	2		1	2	2	1	
<i>Cnemidophorus sacki</i>	14	15	31	27	39	36	22	2
<i>Masticophis flagellum</i>					1			
Total Reptiles	24	29	40	40	53	48	27	2
Soil temperature °C.	26.6		30.8		37.2		41.9	
Air temperature °C.	24.7		26.4		28.0		29.4	
Relative humidity %	57.3		48.5		42.4		40.5	

received general acceptance. Burt (1943, p.351) concisely defines these terms: "Home range then is the area, usually around a home site, over which the animal normally travels in search of food. Territory is the protected part of the home range, be it the entire home range or only the nest." Adequate summaries of other terms used and of animals studied up to 1943 may be found in the papers of Nice (1941), Stickel and Cope (1943), and Burt (1943). The vast amounts of data summarized in these papers and presented in later papers indicate that most, if not all, terrestrial vertebrates demonstrate some form of home range behavior, and many exhibit territoriality. The data also indicate that most animals with definite home ranges make occasional trips outside of them for reasons which are usually undetermined. In calculating home range size, some workers include all of the area within which a given animal is captured, while others delete the area that is only visited occasionally. The definition given by Burt (and others) does not help to resolve the problem. If most animals periodically stray outside of the area in which they are most active, then the wanderings are normal activities and the area covered might be considered as part of the home range. These wanderings frequently appear to be at random with respect to direction and distance, and if included as a part of the home range would devalue the use of home range calculations in comparing animal activities. It is here proposed, therefore, that another term, "home realm," be adopted to include all of the area within which an animal is normally active from day to day. The term "home range" then becomes applicable only to the smaller area in which an animal is *usually* active. The term "territory" remains applicable to the part defended and may be less than, equal to, or greater than the home range, but would not be expected to be greater than the home realm. Thus, the larger area shown for the *Holbrookia maculata* in Figure 1 is the home realm and the smaller area within it is the home range.

ACCOUNT OF SPECIES

Altogether, 133 individuals of 12 species of reptiles and mammals were captured, marked, and released. Of these, 81 were recovered at least once for a total of 252 recoveries. The percentage of the total number of animals marked during each of the five weeks of study was as follows: (1) 66.4%, (2) 9.1%, (3) 15.2%, (4) 5.3%, and (5) 3.3%. One mouse was marked on the last day of study which was the first day of the sixth week.

The maximum number of recoveries for any single animal was 21 for a female *Holbrookia maculata*. Home ranges and realms were calculated for any animal with more than five records (initial capture plus recoveries), except where the records tended to fall along a single, straight line. The records of 11 lizards and one mouse exceeded the arbitrary restrictions. Their home ranges and realms were plotted by marking their points of record on graph paper, joining the outermost points with ruled lines, and calculating the square feet in the enclosed

area. Although, it is highly improbable that any animal moves about in straight lines, this method does provide some estimation of the area covered by an animal in its movements, and a means of comparing areas.

REPTILIA

A total of 114 reptiles of nine species was captured, marked, and released during the study. These consisted of one turtle, 112 lizards of seven species, and one snake. One other snake (*Hypsiglena torquata ochrorhyncha*) was captured in a drift-fence trap, but it was preserved rather than released. The turtle (*Terrapene ornata*), and the one snake (*Masticophis flagellum testaceus*) released, were not recovered. Individuals of three of the lizard species were not recaptured. These included a single greater earless lizard (*Holbrookia texana*), a male and female horned lizard (*Phrynosoma cornutum*), and a single Great Plains skink (*Eumeces obsoletus*). Of the remaining 108 lizards captured and released, 74 were recovered at least once for a total of 230 recoveries.

Holbrookia maculata approximans Baird. Speckled Earless Lizard. Nine females and seven males of this species were marked. Six females and all of the males were recovered at least once for a total of 48 recoveries. There were 22 records for one female, five for another, and nine for one male. The home range of the female with 22 records equalled 0.181 acre and the home realm equalled 0.628 acre (Fig. 1).

The home range of the male was 0.169 acre. The area in which the other female was recorded was 0.349 acre and this possibly included part of the home realm other than the home range. The three home ranges, although all within the quadrat, showed very little overlap. This and the low numbers of this species marked on the quadrat suggest territorial habits.

The nine females varied in length from 50 to 55 mm, average, 52.0 mm; the seven males varied from 54 to 61 mm, average, 56.8 mm.

Sceloporus undulatus consobrinus Baird and Girard. Southern Prairie Lizard. Three females and four males of this species were marked. All were recovered at least once for a total of 22 recoveries. There were six records for one female and nine for a male. The home ranges were calculated at 0.139 acre for the female and 0.132 acre for the male. Body length in the three females varied from 59 to 62 mm; that of the males, from 55 to 63 mm, with an average of 58.0 mm.

Phrynosoma modestum Girard. Round-tailed Horned Lizard. One female and five males of this species were marked and released. Two of the males were recaptured once and the female was recaptured twice. The female was 45 mm in length, and the length of the males varied from 50 to 56 mm with an average of 54.0 mm.

Cnemidophorus sacki. A total of 79 whiptail lizards, 47 females and 32 males, was marked and released over the five weeks of the study. Of these, 51 were recovered at least once for a total of 156 recoveries. Seven whiptails were recovered more than five times and

their activity areas were mapped. The records of two of these proved to be along a trap line and were discarded. Two of the remaining five lizards were recaptured 13 times (the home range of one is shown in Figure 1); one, 11 times; one, eight times; and one, seven times. The minimum home range was calculated at 0.25 acre, the maximum at 0.43 acre, and the average at 0.34 acre. The lizard with the maximum area was recovered one time outside its home range. Addition of this

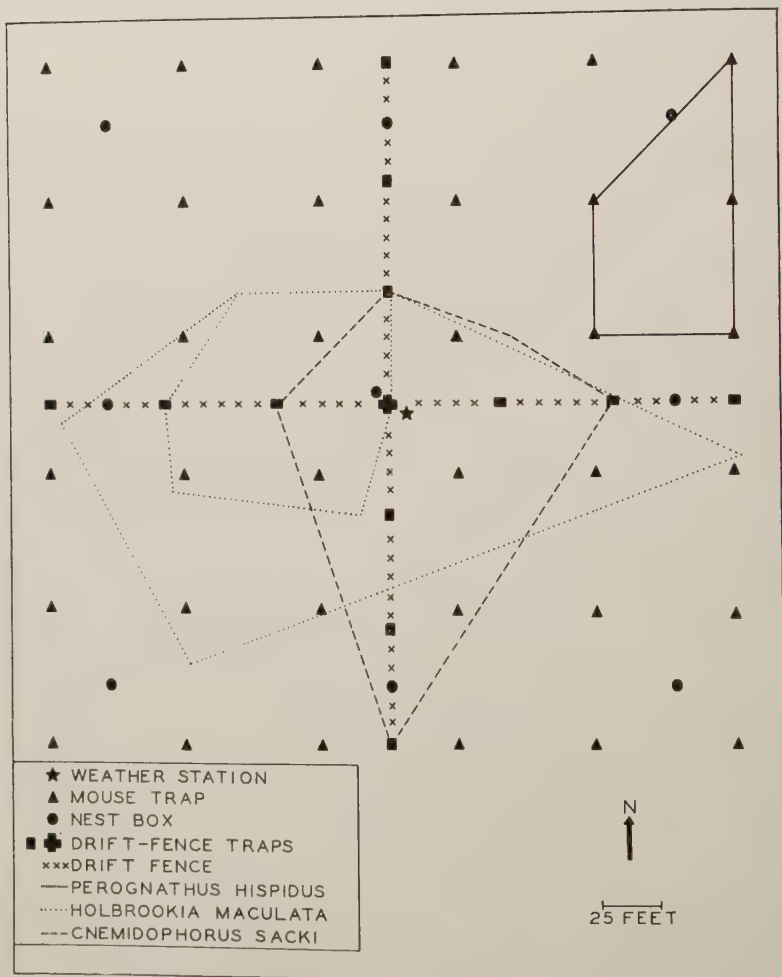


Fig. 1.— Diagram of quadrat lay-out on the Sul Ross State College Ranch during the 1957 summer and of the activity areas of three of the animals studied. The small inner area shown for *Holbrookia maculata* is the home range and the larger area is the home realm. Further explanation of the figure is given in the text.

point to a map of the lizard's movements yields a home realm of 0.76 acre. Milstead (1957b) calculated the home range of an individual of *Cnemidophorus tigris* at Black Gap at 0.26 acre and its home realm at 0.53 acre. When the figures for the home range and the home realm of the Alpine *C. sacki* are compared with those for the Black Gap *C. tigris*, it is found that the figures agree fairly well, proportionally (26/53: 43/87). The home range areas calculated for the two species also compare favorably with the home range areas calculated for *Cnemidophorus sexlineatus* in Kansas by Fitch (1958).

Milstead (1957b) found that the home ranges of several individuals of *C. tigris* showed considerable overlap. This, and the failure of the lizards to patrol their home ranges, was taken as an indication of lack of territoriality. The same observations hold true for *C. sacki* at Alpine.

Fitch (1958) calculated the population density of *C. sexlineatus* in Kansas to have been 65 per acre in 1953, 40 in 1954, 49 in 1955, and 72 in 1956. The 79 individuals of *C. sacki* marked on the Alpine quadrat give a figure of approximately 38 per acre. A Lincoln Index estimation based on the captures and recoveries of the first two days of the study gives a slightly lower figure: 72 lizards total, or 35 per acre. In arriving at these figures by means of a Lincoln Index, the first day (June 6) is used as the precensus period and the second day as the census period. Thus, $A/B : C/D = 24/B : 8/16$; $B = 24 \times 16/8 = 48$. Lincoln Index = $A + B = 24 + 48 = 72$. The symbol "A" represents the number of lizards marked on June 6, "B" the number unmarked on June 6, "C" the number marked on June 6 recaptured on June 7, and "D" the number of unmarked lizards captured on June 7.

Only 51 of the 79 marked lizards were ever recaptured. If it is presumed that transients captured once will not be captured again, that residents will be recaptured at least once, and that the number of recaptures of any individual will be directly proportional to the amount of its home realm lying within the trapping area, then it may be assumed that approximately 51 of the marked lizards were residents and 27 were transients involved in either migration or exploration. A figure of 42 residents is obtained by modifying the Lincoln Index on the basis of the above presumptions. Thus, $A - E/B : C/D - F = 24 - 3/B : 8/16 - 8$; $B = 21 \times 8/8 = 21$. Modified Index = $A - E + B = 24 - 3 + 21 = 42$. Symbols A through D are the same as above. Symbol "E" is the number of lizards marked on June 6 never recovered, and "F" is the number marked on June 7 never recovered. The number of lizards with at least a part of their home realm in the quadrat area may be presumed to be between 42 and 51, or between 20 and 25 resident lizards per acre.

Deaths of six marked lizards were recorded during the study. Three died of overheating in mouse traps, one was swallowed by a snake (*Hypsiglena*) in a drift-fence trap, one was partially eaten by an unknown predator, and one died of unknown causes.

Female *C. sacki* varied from 45 mm to 95 mm in length, average, 66 mm; males, from 55 mm to 88 mm, average, 70.7 mm. No definite size groupings were indicated in the measurements. Fitch (1958) found that young whiptails grow rapidly before and after their first hibernation and reach adult size by the end of their first year. Rapidity of growth decreases with increasing size. Thus, by June or July there is very little size difference between the age groups of yearling lizards and the adults of two or more years.

Observations of the foods and feeding habits of the Alpine *C. sacki* agree in general with those recorded for this species by Milstead (1957a). During the study, whiptails were observed to feed on scorpions (Scorpionida), grasshoppers (Acrididae), termites (Amitermes), candleflies (Lepidoptera), lepidopteran larvae, and ant lions (Myrmelionidae). Several students attempted to follow whiptails in their daily movements and concluded that the lizards travel in small, irregular circles about 20 feet in diameter during foraging. The whiptails appeared to continuously forage in the same general area every day, but within this general area they changed the site of the foraging circle every few days. One whiptail was seen to leap into the air and seize a flying oil beetle (Meloidae) which it later abandoned because of inability to kill the insect, or because of the oil secretion. On one occasion, two whiptails were observed in a drift-fence trap along with a sun spider (Solpugidae). The lizards ignored the arachnid in their efforts to escape from the trap, but the solpugid lashed out at the lizards each time they came close.

Whiptails were also seen to climb into bushes and to dig around stones and plants. While retreating from an observer, one lizard was seen to seek refuge in an ant bed. It quickly emerged with ants clinging to various parts of its body. When picked up, all of the whiptails were heard to emit an audible squeak as recorded for *C. tigris* by Milstead (1959).

The whiptail lizards studied on the Alpine quadrat are representatives of two recognized subspecies, *Cnemidophorus sacki gularis* Baird and Girard and *Cnemidophorus sacki exsanguis* Lowe, which are sympatric at a few localities in the eastern Davis Mountains. The two forms are similar morphologically and in certain behavioral characteristics, but they appear to have different ecological preferences. *C. s. gularis* is typically found in level, prairie areas, while *C. s. exsanguis* is typically found in more rugged habitats (Milstead, 1957a). The localities where the two forms occur sympatrically are near the range extremes of both (western for *C. s. gularis* and eastern for *C. s. exsanguis*), and the habitats are subtypical of both. Whether the two forms include the intergrades of two subspecies, represent two distinct subspecies in an overlap zone, or represent two distinct species is a decision which may be determined only by further study. Should the reader be tempted to draw hasty conclusions, he is reminded that sympatry, especially when it is limited to marginal areas of range, is not by itself sufficient cause for naming two forms as distinct species.

MAMMALIA

Nineteen mammals of three species were captured, marked, and released during the study. Seven of these were recovered at least once for a total of 22 recoveries.

Lepus californicus texanus Waterhouse. Texas Jackrabbit. Individuals of this species were frequently seen on the quadrat, but could not be captured in any of the traps used. Two nests were found during the study and each contained two juveniles. Each nest consisted of scooped-out hollows on the east and west sides of a bush. The young rabbits were found in the west hollow in the mornings and in the east hollow in the evenings. The two juveniles in one nest were marked, but were not recovered.

Perognathus hispidus paradoxus Merriam. Hispid Pocket Mouse. Three females and three males were marked, and three of these were recaptured for a total of eleven recoveries. Two males were recaptured once each and one female was recaptured nine times. The ten records of this female were in four live-mouse traps and the total area (Fig. 1) included only 0.12 acre. It is unlikely that this is the true size of her home range.

Dipodomys merriami merriami Mearns. Four-toed Kangaroo Rat. Five females and six males of this species were captured in live-mouse traps. One female and one male were recaptured twice each, another male was recaptured three times, and another four times. The initial capture and first recapture of the latter male were in the same trap, and the three other recoveries were in an adjacent trap.

Other mammals. Five species of mammals not captured were periodically seen on the quadrat during the study: the cottontail (*Sylvilagus auduboni*), the ground squirrel (*Citellus spilosoma*), the raccoon (*Procyon lotor*), the mule deer (*Odocoileus hemionus*), and the pronghorn antelope (*Antilocarpa americana*). The ground squirrel was the only one of these small enough to be caught in the traps, but that was prohibited by the closure of the traps during daylight hours.

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Melanism in the Poeciliid Fish, *Gambusia affinis* (Baird and Girard)¹

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ABSTRACT: Integumentary melanophores in normally-pigmented *Gambusia affinis* are of two types: a scale melanophore found in the epidermis covering the scales and a stellate micromelanophore which is found in the dermis. Melanistic individuals also possess macromelanophores in the dermis. Melanism appears to be confined to males of the species and the degree of melanism varies greatly. Collections totaling 3,002 fish from three localities in southern Florida contained significantly different percentages of melanistic individuals among the recognizable males. Six F_1 males, progeny of matings of melanistic males with normally-pigmented females, were reared to sexual maturity. All had only normal pigmentation.

The live-bearing top-minnow, *Gambusia affinis* (Baird and Girard), is widely known due to its importance in mosquito control. As Innes (1952) has noted, melanistic individuals occasionally occur in collections of *Gambusia*. This condition is apparently confined to males of the species.

Abnormal melanophores can be the precursors of melanomas (Gordan and Lansing, 1943). Grand, *et al.* (1943) demonstrated essential likenesses in piscine and mammalian melanotic cells *in vitro*. In view of this knowledge and the fact that *Gambusia* occurs so commonly, it is surprising that no works on melanistic *Gambusia* are found in the literature.

The present report deals with the types of integumentary melanophores found in normal and melanistic *Gambusia*, and the frequency of melanistic individuals in collections totaling 3,002 fish from three localities in southern Florida. Some preliminary genetic data are also included.

METHODS

Whole mounts of normal and melanistic skin were made using the alcohol dehydrating series and clearing in terpeneol. Melanophores were measured in the dispersed phase using an ocular micrometer.

Collections were made with a 15 ft. seine of $\frac{3}{8}$ in. mesh (inside measurement, stretched). Since it is probable that some of the very small fish could escape, the collections do not represent a random sample of all sizes. *Gambusia affinis* is 7 to 8 mm, standard length, at birth and the smallest, commonly-occurring size in these collections is 13 mm, although a few fish of 9 to 12 mm were also col-

¹ The writer is grateful to Professors L. C. Gilman, E. R. Rich and L. R. Rivas of the Department of Zoology, University of Miami, Coral Gables, Florida, who offered him aid and helpful criticism during this study.

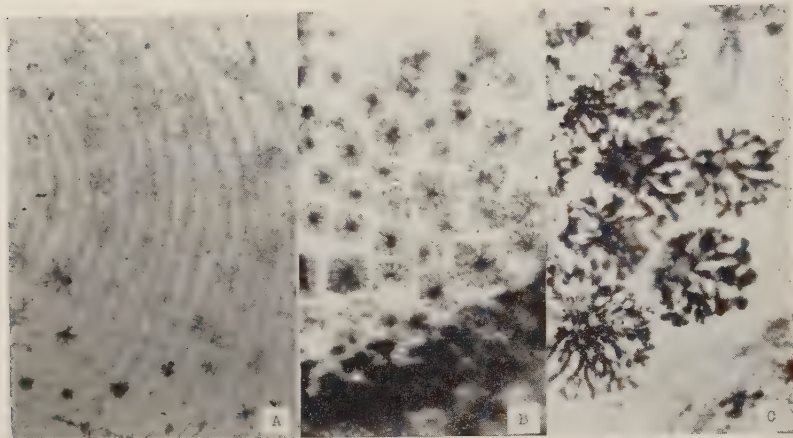


Fig. 1.—Melanophores in *Gambusia affinis*. A. Scale melanophores. B. Dermal micromelanophores. C. Dermal macromelanophores. Magnification 50 $\times$.

lected. Individuals were considered males when any anal fin development beyond that of a normal female was noted.

A gravid, normally-pigmented female was collected and placed in a breeding trap in the laboratory. A stock of virgin females was isolated from her progeny and these were mated to melanistic males. The progeny of these matings were raised to maturity in individual gallon jars.

RESULTS AND DISCUSSION

In normally-pigmented *Gambusia*, two types of melanophores are present in the integument: a scale melanophore (Fig. 1A) which is found in the epidermis covering the scales, and a micromelanophore (Fig. 1B) which is found in the dermis. The scale melanophore has fan-like projections which are morphologically distinct from the stellate projections of the micromelanophores. The scale

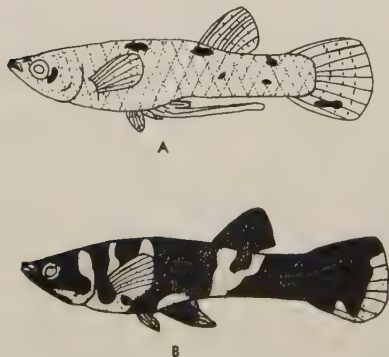


Fig. 2.—Two specimens of melanistic *Gambusia affinis*. A. Mature male, 24 mm standard length. B. Immature male, 18 mm standard length.

TABLE I.—Mean diameters $\pm$ standard error of melanophores in *Gambusia affinis*

Melanophore type	No. measured	M $\pm$ SE
Scale melanophore	35	.056 $\pm$ 0.11 mm
Dermal micromelanophore	50	.074 $\pm$.011 mm
Dermal macromelanophore	19	.146 $\pm$ 0.20 mm

melanophore of *Gambusia* appears to be similar to the scale melanophore described by Gilson (1926) for *Fundulus*, by Goodrich (1927) for *Oryzias*, and by Gordon (1931) for *Platypoecilus*.

The micromelanophore of *Gambusia* is a small cell having many thin, delicate projections; there are also more projections per cell in this than in the other types of melanophores. The general morphology of this cell is almost identical with that of the micromelanophores of *Platypoecilus* as described by Gordon (1931). However, the *Platypoecilus* micromelanophore averaged 1.2 mm in diameter while the micromelanophore of *Gambusia* is .07 mm mean diameter.

In addition to the normal types of melanophores discussed above, melanistic *Gambusia* possess macromelanophores (Fig. 1C) in the dermis. These cells are nearly twice the size of the micromelanophores (Table I) and their morphology is quite distinct. Their projections are much thicker and varicose, and are more dichotomous than those of the micromelanophores.

The number of macromelanophores present in melanistic *Gambusia* appears to vary greatly among individuals. Specimens with only six macromelanophores have been collected, while almost totally-black males have also been taken. The degree of melanism does not appear to vary directly with the degree of sexual maturity, as can be seen by the individuals pictured in Figure 2.

Data on the collections of *Gambusia* from southern Florida are

TABLE II.—Collections of *Gambusia affinis*

Collection	Location	Date	Females and Immature males	Normal males	Melanistic males	Totals
1	Irrigation ditch near mouth of Black Creek, Dade Co., Fla.	April 1, 1958	889	121	2	1012
2	Tamiami Canal, Dade Co., Fla.	June 4, 1958	842	156	12	1010
3	Irrigation ditch near Cutler Rd., Dade Co., Fla.	June 17, 1958	646	330	4	980

TABLE III.—Chi-square test of percentage of melanistic males among total males in each collection

Collection	No. males (n)	No. melanistic males (x)	% melanistic males (p)	(p) (x)
1	123	2	1.6260	3.2520
2	168	12	7.1428	85.7136
3	324	4	1.1976	4.7904
	625	18	9.9664	93.7560

$$\bar{p} = 2.88 \quad \bar{q} = 97.12 \quad \overline{pq} = 279.7056 \quad \overline{p\Sigma x} = 51.84 \quad \text{d.f.} = 2$$

$$\chi^2 = 14.9857 \quad \underline{P} < .01$$

shown in Table II. Collections 1 and 3 came from narrow irrigation ditches with stagnant, turbid water. Collection 2 came from a wide clear stream having apparently good water flow.

The data were tested for significant differences in the percentage of melanistic males among the recognizable males from each locality (Table III).

Chi-square was computed using the Brandt and Snedecor modification (Snedecor 1948) of:

$$\chi^2 = \frac{100(\Sigma px - \frac{\Sigma p}{p} \Sigma x)}{\overline{pq}}$$

where: p = percentage of melanistic individuals among recognizable males collected,

x = number of melanistic individuals among recognizable males collected,

n = number of males in each sample,

$$\bar{p} = \Sigma x / \Sigma n$$

$$\bar{q} = 1 - \bar{p}$$

These percentages differed significantly and Collection 2 is seen to have contributed the aberrant values. Barney and Anson (1921) and Geiser (1924) have shown that sex ratio varies with time and place in *Gambusia*; it is thus not feasible to compare the percentage of melanism among all the fish collected from place to place. Comparing percentage melanism among the recognizable males is also not completely satisfactory since an unknown quantity of immature males is included in the fish classed as females. The error thus introduced

cannot be great, however, since mature and maturing males of 13 to 15 mm, standard length, occurred in all three collections, and a very small proportion of the fish classed as females were below this size range.

A total of 16 F_1 progeny from two matings of melanistic males with normal females were brought to sexual maturity. Six of these were males, all of which were normally-pigmented. These results might appear to negate a hypothesis of holandric inheritance of melanism. However, the expression of the melanistic phenotype may possibly be modified by certain ecological factors, particularly temperature, and since the F_1 males were not reared under controlled physical conditions, these results do not conclusively exclude holandric inheritance. In the same way, differing ecological conditions which may affect expression of the melanistic phenotype, rather than differing gene frequencies, may account for the variation found in the frequency of melanistic individuals in the collections reported here.

In addition to the hypothesis of holandric inheritance, there are, of course, other genetic hypotheses to be investigated.

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The Marsh Flies of Idaho and Adjoining Areas (Diptera: Sciomyzidae)¹

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ABSTRACT: Keys and distributional data are given for the 16 genera and 75 species of marsh flies known to occur in the northwestern states and provinces of Montana, Utah, Idaho, Washington, Oregon, Alberta and British Columbia. Detailed collection records are given only for Idaho, but the place of collection is given for the other states and provinces. A general discussion of Idaho as a habitat for marsh flies is presented, and important collecting stations within the state are described.

INTRODUCTION

Although recent papers by Steyskal (1950, 1954a, 1954b, 1954c, 1954d, 1956, 1957, 1959), Berg (1953), Foote (1959) and Foote *et al.* (1960) present information on one or more species of Sciomyzidae occurring in northwestern North America, there has been no comprehensive publication dealing with the family in the Pacific Northwest since the revisions by Melander (1920) and Cresson (1920). In the present paper are presented keys to the 16 genera and 70 species and subspecies of marsh flies occurring in the northwestern states and provinces of Montana, Utah, Idaho, Washington, Oregon, Alberta and British Columbia. Although detailed distribution records are given only for Idaho, some information on the local occurrence of the flies in other states and provinces is also included.

Papers by Berg (1953), Berg *et al.* (1959), Foote (1959) and Foote *et al.* (1960) present evidence that many, if not all, sciomyzid larvae kill and feed upon aquatic and terrestrial snails. A continuum of feeding habits has been found, with some species having larvae that are free-living aquatic predators, while others have terrestrial parasitoid larvae. Larvae of many species have feeding habits that are intermediate between these two extremes. The author is presently engaged in a study of the biology of the species occurring in the Pacific Northwest and has accumulated additional information on the snail-killing activities of the larvae. However, little of this biological information is included in the present paper because data for some species are still fragmentary and the biology of many species has not yet been investigated.

Acknowledgments.—Although most of the distributional data for Idaho were obtained by the author, several other individuals made important contributions. The members of the Department of Entomology, University of Idaho, have been very co-operative with the sciomyzid survey of the state. H. C. Manis,

¹ Published with the approval of the Director of the Idaho Agricultural Experimental Station as Research Paper No. 484.

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head of the department, by his continuing interest in the study stimulated the publication of this report. W. F. Barr collected specimens in many regions of the state and provided information as to productive collecting sites. A. R. Gittins, survey entomologist, and R. W. Portman, extension entomologist, provided transportation to many localities throughout the state and contributed specimens collected during their travels. Appreciation is also due to several curators of collections in states and provinces surrounding Idaho. George F. Ball (University of Alberta), Frank Hasbrouck (Oregon State University), George F. Knowlton (Utah State University), Maurice T. James (Washington State University) and G. G. E. Scudder (University of British Columbia) freely loaned the specimens under their care. Finally, appreciation is extended to George C. Steyskal, the leading American authority on the Sciomyzidae, for his co-operation in the determination of certain difficult species, especially within the genus *Pherbellia*.

GENERAL ACCOUNT

Located on the western flanks of the Northern Rocky Mountains, the state of Idaho shows a diversity of physiography, climate, life zones, and biotic provinces. Fenneman (1931) recognizes four physiographic provinces within the state. The mountainous sections of northern and central Idaho are in the Northern Rocky Mountain Province. This province is delimited on the south by the lava plains along the Snake River and in the west by the Columbia Plateau. Northward and eastward the province extends beyond the boundaries of the state. The elevation within this large area ranges from less than 3000 feet on the west where the Salmon River leaves the province to over 12,000 feet at Mt. Borah near the southern border. The rocks making up the mountains are almost uniformly resistant, and much of the mountainous terrain is characterized by an accordance of crest levels that appears to have resulted from the dissection of an old plateau surface. Long, linear ranges are relatively uncommon. The valleys are usually steep walled and in some areas form extensive basins (e.g. Stanley Basin north of Sun Valley and the basin surrounding Idaho City.) Near the southern border of the province where the mountains abut against the Snake River lava plains, long, linear valleys separated by ranges of lofty mountains are found. On the border between Idaho and Montana the Bitterroot Range rises to elevations exceeding 9000 feet with an occasional peak rising to 10,500 feet. In the north near the Canadian border the mountains rarely exceed 7000 feet and are separated into more or less north-south ranges by sizeable river valleys.

Lying along the Idaho-Wyoming border is a mountainous area that Fenneman includes in the Middle Rocky Mountain Province. In Idaho this province includes a series of nearly parallel, north-south ranges (e.g. Bear River Range, Caribou Range, Snake River Mountains) that are bounded on the west by the Snake River Plain and the Basin and Range Province. The crests reach elevations between 9000 and 10,000 feet. Located east of the Bear River Range is an extensive marshy plain bordering Bear River and Bear Lake.

The Columbia Plateau Province enters the state from the west and

in southern Idaho includes the extensive area of lava plains located along the Snake River. The rocks underlying this province are mainly lava flows ranging from 10 to 100 feet in thickness. Near the western boundary of the state along the Snake River approximately 4000 feet of lava beds are exposed. In western Idaho lake sediments are interbedded with the lava flows. The topography is generally flat to slightly undulating, although cliffs are abundant along the larger streams and numerous buttes and lava cones project above the general plateau surface. The elevation on the lava plains ranges from less than 2500 feet in the west to nearly 6000 feet in the northeast. Traversing the extensive lava plains is the great canyon of the Snake River. South of this river and near the Oregon border are found the Owyhee Mountains, a north-south range that is about 30 miles long and surrounded by lava plains. The mountains reach elevations exceeding 8000 feet with the plateau surface sloping away in all directions from the high center. Along the western border of Idaho near the southeastern corner of Washington is an area of gently rolling hills called the "Palouse Country." The soil in this region is a very fine textured, deep loess deposit blown in from arid lands to the west.

The southcentral portion of the state extending east to the foot of the Bear River Range is included in the Basin and Range Province. Within this area the topography consists of isolated, parallel ranges separated by broad, arid, nearly level basins. The rocks underlying the basins are mostly sedimentary, while the higher mountains frequently have a core of igneous rocks. At the foot of the mountains are extensive alluvial fans and slopes which gradually merge with the flat plains.

Carter (1941) presents a general account of the climatic conditions existing within the state. He notes that altitude, not latitude, is of primary importance in influencing temperature and precipitation. Lying in a region of prevailing westerly winds, the state is greatly affected by the ameliorating influence of the Pacific Ocean and has a climate milder than its geographic position and altitude would otherwise indicate. The Continental Divide serves as a partial barrier to the cold fronts moving down from the Canadian Northwest. In general, there is a gradual rise in the annual precipitation from the relatively low-lying Columbia Plateau Province to the high mountains of central and eastern Idaho. The average annual precipitation ranges from 10 inches or less along the Snake River to more than 40 inches in the extreme northeastern counties. Much of the state lying in the Panhandle near the Washington-Idaho border receives 20 to 30 inches annually while the southern and eastern counties receive 10 to 20 inches per year. Over practically the entire state January is the wettest month and July and August are the driest. From August on, there is a gradual, but steady rise in the monthly precipitation. Thirty-three percent of the precipitation occurs during the winter months; 27 percent in March-May; 15 percent in June-August and 25 percent during the fall.

The last killing frost usually occurs during May in much of the Panhandle, along the Snake River and in the southern counties. Locally in the Panhandle, at low elevations along the Idaho-Wyoming border and in parts of the interior, the average date occurs in June. At high elevations in mountainous terrain, heavy frosts may occur in every month of the year. The first killing frost in fall comes during August at high elevations along the Idaho-Wyoming border and in parts of the interior, but in the Boise Valley and in much of the Panhandle, it is delayed until October. In the remainder of the state, it usually occurs sometime in September.

According to Dice (1943) four biotic provinces are found in Idaho. The extensive sage-brush covered plains of southern Idaho belong to the Artemisian province. Coinciding with the Northern Rocky Mountain physiographic province is the Montanian province, while the Coloradan province is co-extensive in Idaho with Fennerman's Middle Rocky Mountain Province. The "Palouse Country" is included in the Palousan province. Knowledge of the distribution of sciomyzids in Idaho is still too incomplete to determine whether any of these biotic provinces have characteristic faunas.

Mason (1957) presents a classification of aquatic habitats based on his studies of the marshlands of California. Following his classification, specimens of sciomyzids were taken in Idaho from margins of permanent fresh water lakes, ponds and marshes, vernal pools and marshes and from streamside marshes. Those sciomyzid species whose larvae are aquatic predators (e.g. *Sepedon fuscipennis*) are found predominantly in the more permanent marshy situations such as those found around lakes and ponds. Those species whose larvae attack stranded aquatic snails (e.g., *Atrichomelina pubera*) occur most commonly in habitats where the water level is unstable. The larvae of *Sciomyza* spp. develop in species of *Oxyloma*, the so-called amphibious snails that are found commonly on emergent vegetation in marshy habitats. No sciomyzid known to have its larval stages associated with strictly terrestrial snails has been found in Idaho.

COLLECTING STATIONS

Several collecting stations were established in various habitats throughout the state. As these stations will be utilized in future studies, they are described in some detail below.

Copeland, Boundary County.—This station consists of two small ponds located in borrow pits along both sides of the Great Northern Railway just north of the town. The pond situated on the west side of the tracks is mostly unshaded and has considerable development of emergent vegetation. Its shores are covered with species of rushes, sedges, grasses, shrubs (especially red-osier dogwood, *Cornus sericea* L.) and a few small trees (mostly willows, *Salix* spp. and trembling aspen, *Populus tremuloides* Michx.). Aquatic snails common in the pond are *Lymnaea palustris* (Muller) and *Helisoma* sp. Among the

sciomyzids swept from the herbaceous vegetation bordering the ponds were *Sciomyza simplex*, *Pherbellia griseola* and *Hedroneura rufa*.

The somewhat larger pond east of the tracks contains relatively little emergent vegetation, but is bordered by a dense zone of herbaceous plants composed largely of sedges, jewelweed (*Impatiens aurella* Rydb.), various species of shade-loving asters, nettles (*Urtica* spp.), cocklebur (*Xanthium strumarium* L.), beggar-ticks (*Bidens cernua* L.), rattlesnake-root (*Prenanthes sagittata* Gray) and Joe-pye-weed (*Eupatorium maculatum* L.). Shrubs are abundant, especially the red-osier dogwood, and the margins of the pond are well-shaded by such deciduous trees as willow, cottonwood (*Populus trichocarpa* T. & G.) and box-elder maple (*Acer negundo* L.). In addition to *Lymnaea* and *Helisoma* snails, species of *Gyraulus* and *Physa* are found. Among the more interesting sciomyzids collected around the margins of the pond were *Pherbellia griseola*, *P. vitalis*, *Antichaeta melanosoma* and *Sepedon spinipes americana*.

Eight miles north of Sandpoint, Bonner County.—This is a small, partially wooded swamp situated in a borrow pit between U. S. Highway 95 and the Great Northern Railway. The area is partially shaded by small alders, willows, and box elder maples with an understory composed mostly of young trees and red-osier dogwood. The herbaceous vegetation is lush and forms a dense cover over the permanently saturated soil. Common herbs are bracken fern (*Pteridium aquilinum* var. *languinosum* (Bong.) Fernald), rushes (*Juncus* spp.), sedges (mostly *Carex* sp.), jewelweed, beggar-ticks and cocklebur. In addition to a shallow pond of 8 to 20 feet diameter, there are several small depressions that contain a few inches of water during the spring and early summer. Snails present in the area included *Lymnaea palustris*, *L. humilis* Say, *Physa gyrina* Say, *Gyraulus* sp. and *Oxyloma* sp. Among the more interesting sciomyzids collected by sweeping the hydrophilic vegetation were *Pherbellia schoenherri*, *Renocera cyathiformis*, *Tetanocera plebeia* and *T. unicolor*.

Three miles south of Worley, Kootenai County.—The collecting station is located in a small marshy area lying on the west side of U. S. Highway 95 near a small stream. Standing water up to a foot in depth covers much of the area during spring and early summer, but the marsh becomes completely dry by late July. Along the western margin of the marsh is a mixed stand of second-growth deciduous and coniferous trees. Trembling aspen, willows, and ponderosa pine (*Pinus ponderosa* Dougl.) are especially numerous and offer some shade. Growing in portions of the marsh itself is a dense shrub cover composed mostly of white spiraea (*Spiraea betulifolia* Pall.). Hydrophilic herbaceous vegetation is abundant and is composed of such forms as grasses, rushes, sedges, rice-root (*Fritillaria lanceolata* Pursh), hellebore (*Veratrum viride* Alt.), blue-eyed grass (*Sisyrinchium inflatum* Suksd.) buttercups (*Ranunculus* spp.), marsh cinquefoil (*Potentilla arguta* Pursh), monkey-flower (*Mimulus* sp.), *Downingia elegans* (Dougl.), beggar-ticks, tickseed (*Coreopsis atkinsoniana* Dougl.) and

squaw-weed (*Senecio* sp.). Snails are abundant and usually are stranded on the wet mud as the water recedes during the summer months. Common species present are *Lymnaea palustris*, *L. humilis* and *Physa* sp. Among the more interesting sciomyzids collected were *Pherbellia vitalis*, *Sepedon neili* and *Tetanocera plebeia*.

Robinson's Lake, Latah County.—This is a small, artificial lake located approximately eight miles east of Moscow. The lake was formed during the 1930's by the construction of a dam across a small stream. Although the eastern and western shores are wooded (mostly ponderosa pine), the greater share of the lake is unshaded. The greatest depth is found near the dam at the south end while the north end bordering the inlet stream is shallow and supports a lush growth of emergent vegetation. Here, cat-tails (*Typha latifolia* L.), sedges (mostly *Carex* spp.) and rushes form fairly dense stands. Immersed species abundant in the shallower water near the shoreline include Canada waterweed (*Anacharis canadensis* (Michx.) Planch), hornwort (*Ceratophyllum demersum* L.), water milfoil (*Myriophyllum verticillatum* L.), and pondweed (*Potamogeton* spp.). Duckweed (*Lemna minor* L.) frequently covers the water's surface where the depth does not exceed two feet. Lying along the inlet stream is an extensive mud flat covered by a lush growth of reed canary grass (*Phalaris arundinacea* L.). Aquatic snails are very abundant and include such species as *Lymnaea palustris*, *L. humilis*, *Physa gyrina*, *Helisoma* sp. and *Gyraulus* sp. Among the more interesting species of sciomyzids collected were *Pherbellia grisescens*, *Tetanocera plebeia*, *T. robusta* and *T. soror*.

Dixie, Elmore County.—This station is a relatively open expanse of marshland located approximately one mile southwest of the town. The area is largely unshaded and lies in a shallow depression surrounded by low, sagebrush-covered hills. A small stream meanders through the marsh, but most of the surface water seems to result from seepage along the margins of the hills. Although the soil remains saturated throughout the year, standing water is present only during the spring and early summer. Herbaceous, hydrophilic vegetation is abundant, but is composed mostly of numerous species of sedges and rushes. Other herbs present include blue-eyed grass, duckweed, buttercups, asters, balsam root (*Balsamorhiza* sp.) water-cress (*Rorippa nasturtium - aquaticum* (L.) S. & T.) and marsh cinquefoil. Snails are abundant and include such species as *Lymnaea humilis*, *Physa* sp., *Gyraulus* sp. and *Oxyloma* sp. Interesting sciomyzids collected were *Hedroneura connexa*, *Sepedon borealis*, and *Tetanocera latifibula*.

Stanley Basin, Blaine and Custer Counties.—This is a high mountain valley lying along the headwaters of the Salmon River. The valley is bounded on the west by the Sawtooth Mountains, on the southeast by the Boulder Mountains and on the north by the Salmon River Mountains. The collecting station was established along the east shore of the river near U.S. Highway 93, approximately ten miles

north of Galena Summit. The area sampled includes several small ponds evidently formed by overflow from the main stream. Small alders and willows give some shade, but most of the habitat is unshaded. Aquatic emergent vegetation is abundant and is composed mostly of various species of sedges and rushes along with some cat-tail and water cress. The margins of the ponds support lush stands of sedges, rushes, and grasses along with a variety of other hydrophilic herbs. Shrubs are fairly common with red-osier dogwood and white spiraea being especially numerous. Common snails are *Lymnaea palustris*, *L. humilis*, *Physa* sp. and *Oxyloma* sp. Among the numerous sciomyzids collected by sweeping the herbaceous vegetation were *Sciomyza dryomyzina* (only Idaho record), *Hedroneura connexa*, *Renocera cyathiformis*, *R. johnsoni* and *Tetanocera latifibula*.

Ten miles west of Mack's Inn, Fremont County.—This station is located approximately 100 yards north of a gravel road running between Kilgore and U.S. Highway 20. It consists of a small marsh of less than one-half acre lying in a slight depression on the nearly level plains west of Mack's Inn. Although the water level decreases steadily as summer advances, the soil of the marshy area remains moist throughout the summer. The vegetation consists almost entirely of a fairly dense stand of rushes and sedges. Snails are abundant and are frequently stranded as the water level recedes during the late summer. Species found in the marsh include *Lymnaea palustris*, *L. humilis*, *Helisoma* sp. and *Physa* sp. Among the more interesting sciomyzids collected by sweeping the marsh vegetation were *Atrichomelina pubera*, *Pherebellia grisescens* and *P. vitalis*. Over 500 specimens of *P. vitalis* were collected during an hour of intensive collecting on July 17, 1959.

Swan Lake, Targhee National Forest, Fremont County.—This station consists of a small, senescent lake located on the west side of U.S. Highway 20 approximately 15 miles south of Mack's Inn. The lake does not exceed 10 feet in depth and the greater portion of its expanse is less than two feet in depth. Immersed, floating and emergent vegetation is abundant, and very little open water is present. Immersed plants include Canada waterweed, water milfoil, hornwort, naiad (*Najas flexilis* Willd.) and pondweed. Floating species present, among others, are yellow pond-lily (*Nuphar polysepalum* Engelm.), watershield (*Brasenia Schreberi* Gmel.) and duckweed. Emergent plants form dense stands in the shallower water and include such species as hydrophilic sedges and rushes, arrowhead (*Sagittaria latifolia* Willd.) water plantain (*Alisma Plantago-aquatica* L.) cat-tail and bur-reed (*Sparganium* sp.). The lake is nearly encircled by a forest composed almost entirely of coniferous species. The shallower areas of the lake support a rich population of aquatic snails including *Lymnaea palustris*, *Helisoma* sp., *Physa gyrina* and *Gyraulus* sp. among others. Individuals of the so-called amphibious snail *Oxyloma* sp. are abundant on the leaves and stems of the emergent plants. Some of the more interesting species of sciomyzids collected were

Sciomyza simplex, *Pherbellia nana*, *Pteromicra nigrimana*, *Tetanocera latifibula* and *T. mesopora*.

Bear Lake, Bear Lake County.—The collecting station was located in an extensive marshy area approximately four miles west of the town of Mud Lake and one-half mile north of the gravel road leading east from U.S. highway 89 to the town. The flood plain bordering the Bear River north of the lake is low-lying, poorly drained and includes many extensive marshes. The collecting station was placed at the edge of one of these marshy areas. The marsh is completely unshaded and supports a rich stand of hydrophilic vegetation composed primarily of numerous species of sedges (mostly *Carex* spp.) and rushes. At the time of collection in mid-July the water depth was less than one foot, and extensive areas lacked standing water, although the soil was water-logged. Aquatic snails are abundant and include such common genera as *Lymnaea*, *Physa*, *Helisoma* and *Gyraulus*. Many snails are stranded on the wet soil as the water level recedes during the summer months. A very interesting group of sciomyzid species was taken including some forms not collected elsewhere in the state (e.g., *Pherbellia obtusa* and *Sepedon anchista*).

In addition to the several collecting stations described above, specimens are available from numerous other localities throughout the state. In order to avoid unnecessary repetition in the systematic account these localities are listed by county below.

Bear Lake Co.: Bear Lake, Fish Haven, Montpelier; *Benewah Co.*: Rocky Point on Lake Chatcolet; *Bingham Co.*: Aberdeen; *Blaine Co.*: Gannet, Hailey; *Bonner Co.*: Granite Lake, 12 miles N. of Granite, Sandpoint, Westmond; *Boundary Co.*: Bonners Ferry, Copeland, Priest Lake, Priest River Forest Experiment Station; *Butte Co.*: Arco, near Craters of the Moon National Monument.

Camas Co.: Fifteen miles S. of Fairfield, Hill City; *Canyon Co.*: three miles W. of Parma; *Caribou Co.*: Bancroft, Wayan; *Cassia Co.*: Declo, Elba-Basin Pass, Emery Canyon located 12 miles SE. of Oakley; *Clark Co.*: Kilgore, 2 miles E. of Spencer; *Clearwater Co.*: Elk River, Pierce; *Custer Co.*: Challis, 14 miles N. of Mackay, Stanley Basin approximately 10 miles N. of Galena Summit, Stanley.

Elmore Co.: Dixie, Little Camas Reservoir; *Fremont Co.*: Henry's Lake, 10 miles W. of Mack's Inn, Swan Lake in Targhee National Forest; *Gooding Co.*: Hagerman; *Idaho Co.*: 12 miles S. of Pollock; *Jefferson Co.*: Roberts; *Jerome Co.*: Hazelton; *Kootenai Co.*: Hauser Lake, 3 miles S. of Worley.

Latah Co.: Three miles S. of Deary, 4 miles E. of Genesee, Kendrick, Laird Park near Harvard, Lewiston Grade, Moscow, Moscow Mountain, Robinson's Lake, 5 miles N. of Troy, Vassar Meadows near Deary; *Lemhi Co.*: two miles N. of Gilmore, Salmon; *Lewis Co.*: Craigmont; *Lincoln Co.*: Dietrich, 4 miles E. of Shoshone, Star Lake; *Madison Co.*: Sugar City; *Nez Perce Co.*: Spalding.

Owyhee Co.: Bruneau, Hot Creek Falls; *Payette Co.*: Fruitland; *Power Co.*: Massacre Rocks; *Shoshone Co.*: Kellogg; *Twin Falls Co.*: Clover, Rock Creek Ranger Station in Sawtooth National Forest, Rogerson; *Valley Co.*: Donnelly.

SYSTEMATIC ACCOUNT

The family Sciomyzidae is distinguished from other acalyptrate Diptera by the following combination of characters: costa entire, not broken; subcosta complete, free from vein R_1 distally and ending in the costa; first posterior cell open, not narrowed apically; oral vibrissae absent; postvertical bristles diverging; one or more tibiae with preapical bristles; femora with bristles.

Certain structural characteristics require explanation before the keys to genera and species can be used properly. Species of the subfamily Sciomyzinae have a strong bristle on the propleuron immediately above the base of the fore coxa, but in the genus *Atrichomelina* this bristle is very fine and thin. In the Tetanocerinae the propleura have only small clusters of short, fine hairs. The preapical tibia bristles may be single (Fig. 11) or double (Fig. 12) and may at times be confused with the apical bristles. Usually, however, they are distinctly separated from the apical bristles and easily recognizable. The vellar bristles, if present, are situated on a low, narrow ridge on the pteropleuron just below the base of each wing. The suprspiracular convexity is a low swelling located antero-dorsad of the posterior spiracle and posterior to the base of each wing. Other structures mentioned in the keys are illustrated and need no additional comment here.

In certain genera, especially *Pherbellia* and *Dictya*, the definitive species characters are found in the male genitalia. In order to view the important structures, the posterior tip of the abdomen must be removed, placed in hot 10 per cent potassium hydroxide for a minute or so, washed in water and then spread apart. In the present paper an attempt has been made in the keys to use non-genitalic characters as much as possible, but in the genus *Dictya* this has proved impossible and reference to the male genitalia has been necessary. For figures of the male genitalia in other genera of sciomyzids the reader should refer to the numerous papers by Steyskal.

The genus *Limnia* is in great need of revision, but until that has been done it seems best merely to modify Melander's (1920) key even though some of his species are obviously composite forms. The genus *Pherbellia* is currently being revised by Steyskal, and six new species discovered in Idaho will be described by him in a future publication.

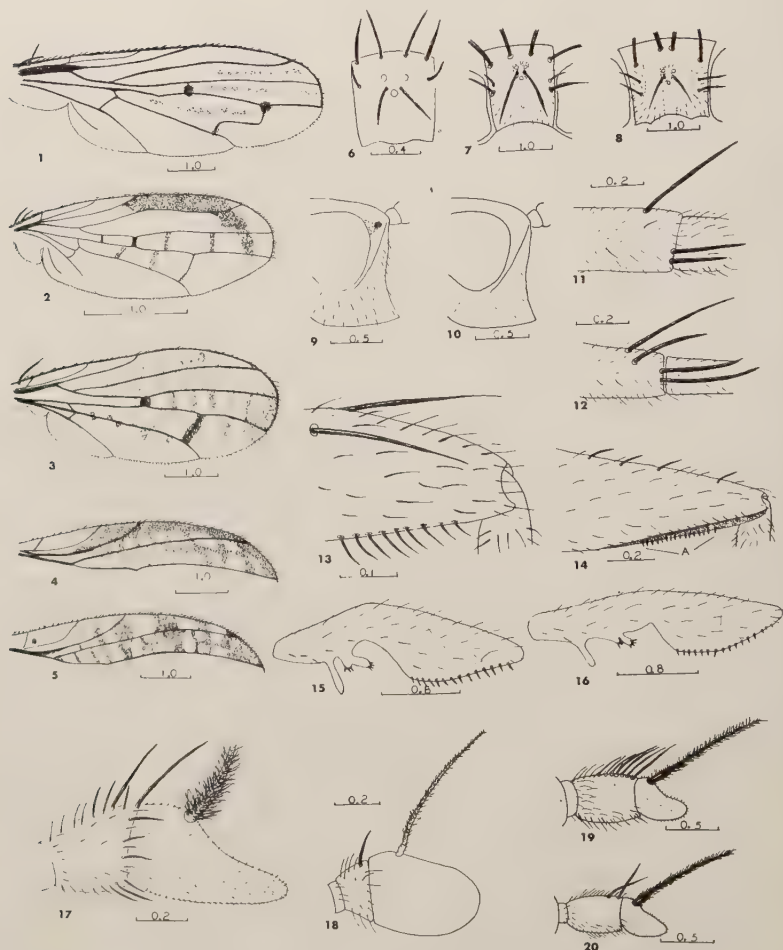
KEY TO GENERA

1. Propleuron with strong bristle present above base of fore coxa, if bristle is inconspicuous then first segment of fore tarsi is whitish and contrasts strongly with remaining segments (Sciomyzinae) 2
- Propleuron without strong bristle; first segment of fore tarsi not strongly contrasting with remaining segments (Tetanocerinae) 6
2. Fore tibiae with two preapical bristles *Sciomyza* Fallén
- Fore tibiae with one preapical bristle 3
3. Anal vein not reaching wing margin; body length under 2.5 mm *Colobaea* Zetterstedt (one sp. - *americana* Steyskal)

- Anal vein clearly reaching wing margin; body length usually over 2.5 mm 4
4. Propleural bristle inconspicuous; first segment of fore tarsi whitish, fore coxae without bristles *Atrichomelina* Cresson (one sp. - *pubera* Loew)
- Propleural bristle well-developed; fore coxae with one or more strong bristles 5
5. Body mostly shining black; frons usually entirely shining *Pteromicra* Lioy
- Body never shining black, usually grayish to yellowish in color; frons not wholly shining *Pherbellia* Desvoidy
6. Vallar bristles present 7
- Vallar bristles absent 8
7. Arista with blackish hair; midfrontal stripe very narrow *Trypetoptera* Hendel (one sp. - *canadensis* Macquart)
- Arista with whitish hair or pubescence; midfrontal stripe broader, about one-third width of frons *Limnia* Desvoidy
8. Ocellar bristles absent, postocellar bristles well-developed 9
- Both ocellar and postocellar bristles well-developed 10
9. Frons with two fronto-orbital bristles; posterior cross vein bisinuate *Hedria* Steyskal (one sp. - *mixta* Steyskal)
- Frons with only one fronto-orbital bristle; posterior cross vein arcuate *Sepedon* Latreille
10. Hind tibiae with two strong preapical bristles (Fig. 12) *Antichaeta* Haliday
- Hind tibiae with only one strong preapical bristle (Fig. 11) 11
11. Second antennal segment less than one-third length of third segment (Fig. 18) *Renocera* Hendel
- Second antennal segment at least one-half length of third segment 12
12. Arista with long blackish hairs 13
- Arista with whitish hairs or pubescence 15
13. Wings mostly hyaline, usually without dark reticulations; body uniformly yellowish to reddish-brown; mesopleura bare; face without central black spot *Tetanocera* Dumeril
- Wings heavily marked with blackish spots and reticulations; body brown with numerous blackish spots and elongate markings; mesopleura with bristles 14
14. One fronto-orbital bristle; face with central black spot *Dictya* Meigan
- Two fronto-orbital bristles; face without central black spot *Hoplodictya* Cresson (one sp. - *spinicornis* Loew)
15. Presutural dorsocentral bristle absent; posterior cross vein strongly bisinuate; wings with dark shadings, but never reticulate with black (Fig. 1) *Hedroneura* Hendel
- Presutural dorsocentral bristle present; posterior cross vein arcuate; wings densely reticulate with black *Dictyacium* Steyskal (one sp. - *firmum* Steyskal)

Genus *Pherbellia* Desvoidy

1. Mid-frontal stripe long, reaching at least two-thirds distance to anterior margin of frons (Fig. 6) 2
- Mid-frontal stripe shorter, reaching approximately one-half distance to anterior margin of frons *schoenherri* (Fallén) 4
2. Wings heavily spotted with black *schoenherri* (Fallén) 3
- Wings mostly hyaline *tenuipes* (Loew)
3. Mesopleura bare; two parafrontal bristles



Figs. 1-20.—Anatomical structures important to identification (all measurements in mm). 1.—Wing of *Hedroneura connexa* Steyskal. 2.—Wing of *Pherbellia nana* (Fallén). 3.—Wing of *Tetanocera valida* Loew. 4.—Costal area of wing of *Limnia pubescens* (Day). 5.—Costal area of wing of *Limnia boscii sparsa* (Loew). 6.—Frontal region of *Pherbellia grisescens* (Meigen). 7.—Frontal region of *Tetanocera ferruginea* Fallén. 8.—Frontal region of *Tetanocera plebeia* Loew. 9.—Lateral view of head of *Tetanocera nanciae* Brimley. 10.—Lateral view of head of *Tetanocera mesopora* Steyskal. 11.—Hind tibia of *Renocera cyathiformis* Melander. 12.—Hind tibia of *Antichaeta testacea* Melander. 13.—Hind femur of *Tetanocera montana* Day. 14.—Fore femur of *Pteromicra nigrimana* Meigen; a, pecten. 15.—Hind femur of *Sepedon anchista* Steyskal. 16.—Hind femur of *Sepedon armipes* Loew. 17.—Antenna of *Tetanocera soror* Melander. 18.—Antenna of *Renocera cyathiformis* Melander. 19.—Antenna of *Limnia pubescens* (Day). 20.—Antenna of *Limnia boscii sparsa* (Loew).

- Mesopleura with setae over most of surface; one parafrontal bristle
 *griseus* (Meigen)
4. Mesopleura with row of short bristly hairs along posterior margin 5
 Mesopleura bare 6
5. Wings with costal border yellow, costa, first and second veins yellowish,
 remaining veins brown; pteropleura with short bristly hairs only
 *albocostata* (Fallén)
 Wings without yellowish costal border, all veins brown; pteropleura with
 two conspicuous bristles in addition to shorter bristly hairs
 *griseola* (Fallén)
6. Marginal cell of wing extensively darkened, submarginal cell with dark
 cloud near apex, first posterior cell with approximately three transverse
 dark bars (Fig. 2) *nana* (Fallén)
 Wing membrane mostly hyaline, never with numerous transverse bars in
 first posterior cell 7
7. Anterior legs extensively black; thorax mostly grayish *vitalis* (Cresson)
 Anterior legs reddish-brown, thorax reddish-brown *obtusa* (Fallén)

Genus *Pteromicra* Lioy

1. Fore femora without pecten (series of closely spaced spinules located
 apically on antero-ventral side of femora); pteropleura with at least two
 longer bristles in addition to shorter bristly hairs; basal segment of fore
 tarsi whitish *perissa* Steyskal
 Fore femora with pecten (Fig. 14); pteropleura with cluster of short,
 bristly hairs only; basal segment of fore tarsi blackish 2
2. Palpi wholly yellow; one fronto-orbital bristle 3
 Palpi blackish, at least apically 5
3. Thorax wholly black, head mostly black *nigrimana* (Meigen)
 Thoracic pleura mostly yellowish, head frequently extensively yellow 4
4. Wing cross veins not darkened; last segment of fore tarsi of female whitish
 *apicata* (Loew)
 Cross veins bordered with grayish; last one or two (male) or three
 (female) segments of fore tarsi whitish *pectorosa* (Hendel)
5. Arista whitish, third antennal segment black; apical two or three segments
 of fore tarsi whitish *leucothrix* Melander
 Arista blackish, third antennal segment reddish; fore tarsi wholly black
 *melanothrix* Melander

Genus *Sciomyza* Fallén

1. Mesopleura with at least two strong bristles posteriorly in addition to
 numerous shorter bristly hairs; ventral half of pleura pruinose; dorsum of
 mesonotum grayish with four darker stripes; fore femora usually wholly
 yellow *simplex* Fallén
 Mesopleura with only few fine, short hairs posteriorly; ventral half of
 pleura not pruinose, mesonotal dorsum shining reddish-brown; fore
 femora usually blackened on apical half or more *dryomyzina* Zetterstedt

Genus *Antichaeta* Haliday

1. Body mostly shining black *melanosoma* Melander
 Body reddish yellow, never shining black 2
 Body reddish yellow, never shining black *sp. A.*
2. Third antennal segment yellow basally, blackish apically 3
 Third antennal segment wholly yellow *robiginosa* Melander
3. Thoracic dorsum grayish to blackish *testacea* Melander
 Thoracic dorsum yellowish

Genus *Dictya* Meigen

MALES

1. Surstylus with apical brush of long bristles (Fig. 21) 2
 Surstylus with short bristles only 3
2. Pregonite with preterminal lobe (Fig. 21) *pictipes* (Loew)
 Pregonite without preterminal lobe (Fig. 22) *borealis* Curran
3. Pregonite with expanded preterminal lobe (Fig. 24) 4
 Pregonite gradually tapering, without preterminal lobe (Fig. 26) 6
4. Pregonite short, strongly bent, preterminal lobe reduced to small point (Fig. 25) *incisa* Curran
 Pregonite longer, not strongly bent, preterminal lobe well-developed 5
5. Preterminal lobe long and narrow in anterior view (Fig. 23) *stricta* Steyskal
 Preterminal lobe broadly expanded (Fig. 24) *expansa* Steyskal
6. Prosternum with hairs *umbroides* Curran
 Prosternum bare *montana* Steyskal

Genus *Hedroneura* Hendel

1. Wing with brownish cloud around apex of second vein; fore femur with strong bristles on ventral surface *rufa* (Panzer)



Figs. 21-30.—Male genitalia of various species (all measurements in mm; figures modified from Steyskal, 1950, 1954d and 1959). 21.—*Dictya pictipes* (Loew). 22.—*D. borealis* Curran. 23.—*D. stricta* Steyskal. 24.—*D. expansa* Steyskal. 25.—*D. incisa* Curran. 26.—*D. montana* Steyskal. 27.—*Sepedon neili* Steyskal. 28.—*S. lignator* Steyskal. 29.—*Tetanocera plebeia* Loew. 30.—*T. nanciae* Brimley.

Wing without brownish cloud around apex of second vein (Fig. 1); fore femur without strong bristles on ventral surface *connexa* Steyskal

Genus *Limnia* Desvoidy

1. Brown costal border of wing interrupted by clear spots (Fig. 5) *boscii sparsa* (Loew)
Brown costal border not interrupted by clear spots (Fig. 4) 2
2. Second antennal segment much longer than third segment and with several long bristles above (Fig. 19) *pubescens* (Day)
Second antennal segment only slightly longer than third segment, usually only bisetose above (Fig. 20) 3
3. Posterior cross vein nearly perpendicular; prescutellar bristles vestigial or wanting 4
Posterior cross vein distinctly sinuate; prescutellar bristles more or less well-developed 5
4. Wing with brown costal border ending at apex of third vein; mesonotal vittae faint *costalis brevicostalis* Melander
Wing with brown costal border continuing to or beyond apex of fourth vein; mesonotal vittae conspicuous *costalis vittata* Melander
5. Front wider than long; wing spots nearly hyaline; male with posterior surface of hind femora strongly spinose *saratogensis armipes* Melander
Front square or longer than wide; male with posterior surface of hind femora weakly spinose *saratogensis saratogensis* (Fitch)

Genus *Renocera* Hendel

1. Humeral bristle present; prosternum with setae; one fronto-orbital bristle *cyathiformis* Melander
Humeral bristle lacking; prosternum bare; two fronto-orbital bristles *johnsoni* Cresson

Genus *Sepedon* Latreille

1. Supraspiracular convexity of metathorax bare *fuscipennis* Loew
Supraspiracular convexity with numerous black hairs 2
2. Middle of face bare, only parafacies with black hair *spinipes americana* Steyskal
Middle of face with scattered black hairs 3
3. Second antennal segment distinctly compressed; body over 7.5 mm in length *praemiosa* Giglio-Tos
Second antennal segment slender, less compressed; body less than 6.0 mm in length 4
4. Hind femur of male with deep indentation on ventral surface, hind femur of female without indentation; abdomen brown, usually with only slight indication of bluish color 5
Hind femora of both sexes without indentation on ventral surface, abdomen often with distinct bluish reflection on dorsal surface 8
5. Frons with only very slight indication of black parafrontal spots; basimedial prong on ventral surface of hind femur of male distinctly bifid (known only from California) *bifida* Steyskal
Frons with densely black parafrontal spots 6
6. Subbasal prong on ventral surface of hind femur of male much closer to basimedial prong than to base of femur (Fig. 15); orbito-antennal spots of both sexes with brownish borders *anchista* Steyskal
Subbasal prong on hind femur of male about equidistant from base of femur to basimedial prong; orbito-antennal spots of both sexes large, wholly black 7

7. Parafrontal black spots very large, reaching nearly to vertex; length of subbasal prong on hind femur of male less than one-half width of femur, (known only from Snoqualmie Pass, Washington) *melanderi* Steyskal
Parafrontal spots small, not extending halfway to vertex, length of subbasal prong more than one-half width of hind femur (Fig. 16) *armipes* Loew
8. Pruinose median stripe on face blunt at apex, not reaching oral margin; body dark colored with distinct bluish reflection; prosternum with five or fewer hairs on each side *borealis* Steyskal
Pruinose median stripe on face extending as a point to oral margin; body usually browner; prosternum with more than five hairs on each side 9
9. Male genitalia as figured (Fig. 28) *lignator* Steyskal
Male genitalia as figured (Fig. 27) *neili* Steyskal

Genus *Tetanocera* Duméril

1. Posterior side of middle femur with more than one bristle toward apex, usually three 2
Posterior side of middle femur with only one bristle or completely lacking bristles near apex 3
2. Prosternum with setae *robusta* Loew
Prosternum bare *annae* Steyskal
3. Posterior side of middle femur with single bristle near apex 4
Posterior side of middle femur without bristles near apex 8
4. Hairs on parafacies extending well above midpoint between lower margin of eye and base of antenna (Fig. 9) black orbito-antennal spot present 5
Parafacial hairs not reaching midpoint between lower margin of eyes and antennal bases (Fig. 10) 6
5. Fourth vein with one or more stump veins *vicina* Macquart
Fourth vein without stump veins; male genitalia as figured (Fig. 30) *nanciae* Brimley
6. Arisital hairs very dense and black; orbito-antennal spot usually large and black *obtusifibula* Melander
Arisital hairs scattered and somewhat sparse; orbito-antennal spot usually faint or lacking 7
7. Bristles on posterior surface of fore femur usually at least as long as width of femur *mesopora* Steyskal
Bristles on posterior surface of fore femur short; about one-half width of femur *latifibula* Frey
8. Hind femur with a posterodorsal bristle opposite preapical bristle (Fig. 13) 9
Hind femur without posterodorsal bristle 11
9. Fourth vein with stump veins *rotundicornis* Loew
Fourth vein without stump veins 10
10. Parafrontal stripes broad and strongly shining (Fig. 8); second posterior cell with dark cloud; medifacies of female shining; male genitalia as figured (Fig. 29) *plebeia* Loew
Parafrontal stripes narrow; second posterior cell hyaline; medifacies of female pruinose *montana* Day
11. Wing membrane with numerous brown spots (Fig. 3) *valida* Loew
Wings without brown spots in membrane 12
12. Frons largely shining, midfrontal stripe broadly triangular *unicolor* Loew
Frons mostly dull, midfrontal stripe narrow, parallel-sided 13
13. Anterior margin of front slightly raised and strongly shining, connecting midfrontal and parafrontal stripes anteriorly *silvatica* Meigen

- Anterior margin of front flattened, not shining14
14. Parafrontal stripes broad, strongly shining (Fig. 8); second posterior cell usually with dark cloud on membrane; medifacies of female shining; male genitalia as figured (Fig. 29)*plebeia* Loew
- Parafrontal stripes narrow (Fig. 7); medifacies of female pruinose15
15. Midfrontal stripe narrow, not reaching anterior margin of frons (Fig. 7); wings without stump veins*ferruginea* Fallén
- Midfrontal stripe broader, clearly reaching anterior margin of frons16
16. Arisal hairs dense and black, third antennal segment distinctly concave dorsally (Fig. 17)*soror* Melander
- Arisal hairs sparse, paler, third antennal segment usually not concave dorsally17
17. Blackish orbito-antennal spot present; wings without stump veins*spirifera* Melander
- Orbito-antennal spot absent; wings with stump veins on fourth vein*nigricosta* Rondani

DISTRIBUTION RECORDS

Most of the distributional data presented are based on specimens examined by the author, but in some instances significant records available in the literature are included. If a year is not listed, the specimens were collected during 1959. Unless otherwise indicated, the records were obtained by the author. For Idaho, all collection data are given, but for the other northwestern states and provinces only the place of collection is listed.

SCIOMYZINAE

Atrichomelina pubera (Loew).—Foote *et al.* (1960) state that the larval stages are associated with pulmonate aquatic snails that have been stranded by a receding water level. At Robinson's Lake large numbers of larvae were discovered in *Physa gyrina* snails that were exposed on the wet mud. IDAHO: Robinson Lake, September 28, 1959, May 11; 5 miles N. of Troy, September 6, 1958; 2 miles E. of Spencer, July 15, 1956 (W. F. Barr); Star Lake, July 4 (D. L. Bishop); 10 miles W. of Mack's Inn, July 17. UTAH: Dry Lake. WASHINGTON: Pullman. OREGON: near Corvallis, Klamath Falls, Salem-Albany, Philomath, Newport. ALBERTA: Medicine Hat.

Sciomyza dryomyzina Zetterstedt.—A single specimen collected on July 22 in the Stanley Basin, 10 miles N. of Galena Summit constitutes the only record for the state. In Alaska, Berg (1953) reared an adult from a larva found in the marsh-inhabiting snail *Oxyloma decampi gouldi* (Tyron). At the collecting station in Stanley Basin, *Oxyloma* snails are abundant. Apparently the only previous record for the species in North America is Alaska (Steyskal, 1954).

Sciomyza simplex Fallén.—Foote (1959) reared adults from larvae feeding in *Oxyloma* snails. In Idaho the species was found only in marshes that contained large populations of *Oxyloma*. IDAHO: Bonners Ferry, August 13, 1958; Bancroft, August 3, 1958; Swan Lake, July 18; Bear Lake, July 10. MONTANA: Hill Co. UTAH: Dry Lake. OREGON: Klamath Falls. ALBERTA: Medicine Hat. Cooking Lake. BRITISH COLUMBIA: Agassiz, Nicola, Kamloops.

Pherbellia albocostata (Fallén).—Not yet recorded from Idaho. WYOMING: Jenny Lake in Great Teton National Park. ALBERTA: Banff.

Pherbellia griseola (Fallén).—Common in marshes having a water level that gradually recedes as summer advances. IDAHO: Copeland, June 6; 3 miles S. of Worley; Robinson Lake, May 11; Vassar Meadows, June 6; 3 miles S. of Deary, May 14; Donnelly, August 30, 1952 (W. F. Barr). UTAH: Logan Canyon.

Pherbellia grisea (Meigen).—Common, but rarely abundant, in open marshes throughout the state. IDAHO: Robinson Lake, late August and early September, 1958, May 11; Hazelton, September 7, 1954 (W. F. Barr); 4 miles E. of Shoshone, May 22; 10 miles W. of Mack's Inn, July 16; Henry's Lake, July 17. UTAH: Snowville, Hooper, Tremonton, Logan, Elberta, Burbank. WASHINGTON: White Bluffs, O'Sullivan Dam. OREGON: Butte Falls. ALBERTA: Orion, Medicine Hat.

Pherbellia nana (Fallén).—Common to abundant in open marshes throughout the state. IDAHO: Three miles S. of Worley, June 2; Robinson Lake, late August, 1958; Bruneau, June 25; 15 miles S. of Fairfield, May 21; 4 miles E. of Shoshone, May 22; 14 miles N. of Mackay, May 31 (W. F. Barr); Salmon, May 25, 2 miles E. of Spencer, July 15, 1956 (W. F. Barr); 10 miles W. of Mack's Inn, July 17; Swan Lake, July 18; Bear Lake, July 10. UTAH: Ogden, Richmond, Huntsville, Providence, Pleasant Grove, Brigham, Nephi, Hooper, Woodcross, Bluffdale, Logan Canyon, Cotton. WASHINGTON: White Bluffs, Willow Creek near Lagrosse. OREGON: Pringle Falls W. of Lapine, Prospect, Prineville, 20 miles S. of Bend, Seappoose, 12 miles S. of Corvallis, near Ukiah. ALBERTA: Edmonton.

Pherbellia obtusa (Fallén).—Recorded from Bear Lake on July 19 when approximately 60 adults were taken during a two-hour search of the marsh. ALBERTA: Red Deer.

Pherbellia schoenherri (Fallén).—Occasionally common in unshaded marshes throughout the state. IDAHO: 8 miles N. of Sandpoint, June 1; 3 miles S. of Worley, July 8; Troy, September 6, 1958; 4 miles E. of Genesee, May 13; Dixie, April 17 (W. F. Barr); Hagerman, April 12; 2 miles W. of Gannett, May 22; 14 miles N. of Mackay, May 31 (W. F. Barr). WYOMING: Jenny Lake in Great Teton National Park. UTAH: Logan Canyon. OREGON: 27 miles E. of Prineville, Summit Prairie. ALBERTA: Medicine Hat, Cooking Lake. BRITISH COLUMBIA: Sorenson Lake near Caribou.

Pherbellia tenuipes (Loew).—Not yet discovered in Idaho, but reported from Terrace, British Columbia, by Steyskal (personal communication).

Pherbellia vitalis (Cresson).—Abundant throughout the state in marshes having a water level that recedes gradually during the summer. IDAHO: Copeland, June 1; 8 miles N. of Sandpoint, June 1; 3 miles S. of Worley, May 12, June 2; Moscow, April 8, 1936 (R. E. Miller), May 7; Robinson Lake, late August, 1958, May 11; Vassar Meadows, May 6; 3 miles S. of Deary, May 14; 12 miles S. of Pollock, June 26; Bruneau, June 25; Hagerman, June 20; 15 miles S. of Fairfield, May 21; Hill City, August 27, 1926 (R. W. Haegle); near Craters of Moon National Monument, July 30, 1958 (A. R. Gittins); 10 miles W. of Mack's Inn, July 17; Swan Lake, July 18; Henry's Lake, July 17; Bear Lake, July 10. UTAH: Kanesville, Dry Lake, Hooper, West Jordan, Joseph, Benson, Slaterville. WASHINGTON: Hanford Works, Lind Lake, Paha, Field Springs State Park, Wawawai. Pullman, White Bluffs, O'Sullivan Dam. OREGON: Butte Falls, Cold Springs, St. Helens.

Pteromicra apicata (Loew).—Not yet discovered in Idaho, but reported from Washington by Melander (1920).

Pteromicra leucothrix Melander.—Not yet discovered in Idaho, but reported from Orcas Island, Washington by Melander (1920).

Pteromicra melanothrix Melander.—Not yet discovered in Idaho, but reported from Yellowstone Lake, Wyoming by Melander (1920).

Pteromicra nigrimana (Meigen).—Common to abundant in grass-sedge marshes that become partially dry as summer advances. IDAHO: Bonners Ferry, early September, 1958; 12 miles N. of Granite, July 8; 4 miles E. of Shoshone, June 19; 14 miles N. of Mackay, May 31 (W. F. Barr); Swan Lake, July 18, Bear Lake, July 19. WYOMING: Yellowstone Lake. WASHINGTON: Pullman.

Pteromicra pectorosa (Hendel).—Not yet discovered in Idaho, but reported from the extreme northwestern corner of California by Steyskal (1957).

Pteromicra perissa Steyskal.—Not yet discovered in Idaho, but reported from Buffalo Peaks Area in Chaffee and Parks Counties, Colorado, by Steyskal (1957).

Colobaea americana Steyskal.—Not yet discovered in Idaho, but reported from Aweme, Manitoba, by Steyskal (1954a).

TETANOCERINAE

Antichaeta melanosoma Melander.—A single male taken along margins of easternmost pond at Copeland on July 1 constitutes the only Idaho record. Apparently this is a new record for the Pacific Northwest as all previously known specimens were taken in the northeastern states.

Antichaeta robiginosa Melander.—Not yet discovered in Idaho. OREGON: Roberts. The holotype was collected at Three Forks, Montana (Melander, 1920).

Antichaeta testacea Melander.—Fairly common in marshes during late May and June. IDAHO: 4 miles E. of Shoshone, May 22; Gannet, May 22; Elba-Basin Pass, June 22. UTAH: Parowan, Midvale, Payson. Holotype collected in Galatin County, Montana (Melander, 1920).

Antichaeta sp. A.—IDAHO: Eight miles N. of Sandpoint, June 1.

Dictya borealis Curran.—Not yet discovered in Idaho, but reported from Manitoba and Saskatchewan by Steyskal (1954d).

Dictya expansa Steyskal.—In Alaska, Berg (1953) reared larvae on aquatic pulmonate snails. In Idaho, the species was common to abundant in the more permanent marshes that had large populations of *Physa* sp. and *Lymnaea palustris*. IDAHO: Bonners Ferry, August 18, 1958; Hauser Lake, May 22 (H. W. Homan); 3 miles S. of Worley, May 26, July 8; Robinson Lake, September 15, 25, 1958; Spaulding, May 17, 1954 (W. F. Barr); 3 miles W. of Parma, June 19 (H. W. Homan); Bruneau, May 25; Roberts, August 1, 1958. WASHINGTON: Pullman, Ilwaco, White Bluffs. OREGON: Cold Springs.

Dictya incisa Curran.—Not yet discovered in Idaho, but reported from Utah (Leeds, Mirror Lake, St. George, Spanish Fork, Uintah Mts.) and Washington (Yakima) by Steyskal (1954d).

Dictya montana Steyskal.—Common to abundant in permanent marshes throughout the state. IDAHO: Eight miles N. of Sandpoint, July 8; Kellogg, August 14, 1926 (R. W. Haegeler); Robinson Lake, August 14, September 6, 1958, September 25; Vassar Meadows, May 6; Pierce, August 4, 1926 (R. W. Haegeler); Dixie, April 17; Hagerman, May 23; 4 miles E. of Shoshone, May 22, June 1, July 10 (D. L. Bishop); Clover, August 25, 1953 (A. R. Gittins); Elba-Basin Pass, June 26; 2 miles W. of Gannet, May 22, July 22; Stanley Basin, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); Fish Haven, May 21, 1949 (G. F. Knowlton). UTAH: Ogden, Brigham, Benson, Logan, Logan Canyon, Payson, Slaterville, Hooper, Riverdale, Eden, Farmington, Duchesne.

WASHINGTON: Pullman, O'Sullivan Dam, Anacortes. OREGON: Butte Falls, Deschutes River near Redmond, 10 miles SE. of Prineville, Odell Lake, near Corvallis, 10 miles N. of Seneca, Medford.

Dictya pictipes (Loew).—Not yet discovered in Idaho, but reported from Ravalli County, Montana by Steyskal (1954d).

Dictya stricta Steyskal.—Three specimens from 20 miles S. of Salmon and five specimens from two miles N. of Salmon taken on May 25 constitute the Idaho records. All specimens were taken in wooded situations (mostly willows, alders, and cottonwoods) with some standing water present. MONTANA: Three Forks. UTAH: Richmond.

Dictya umbroides Curran.—Not yet discovered in Idaho, but reported from northern British Columbia by Steyskal (1954d).

Dictyacium firmum Steyskal.—IDAHO: Priest River Forest Experiment Station, August 14, 1958 (A. R. Gittins); Craigmont, July 22, 1952 (W. F. Barr).

Hedria mixta Steyskal.—Not yet discovered in Idaho, but reported from Alberta (Wabamun, Nordegg) and Saskatchewan (Waskesiu Lake) by Steyskal (1954a).

Hedroneura connexa Steyskal.—Fairly common in the more permanent marshes across the southern part of the state. IDAHO: Donnelly, August 12, 1952 (S. E. Knapp); Dixie, June 20, 1953 (W. F. Barr), April 12, 19; Rock Creek Ranger Station, Sawtooth National Forest, June 20; Stanley Basin, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); Bancroft, August 3, 1958. UTAH: Logan Canyon, Wasatch. OREGON: 10 miles S. of Corvallis, 10 miles N. of Seneca. ALBERTA: Banff.

Hedroneura rufa Panzer.—In Alaska, Berg (1953) discovered that the larval stages are predaceous on aquatic pulmonate snails. In Idaho, third-instar larvae were found at the north end of Robinson Lake during late August, 1958. IDAHO: Copeland, July 1; Bonners Ferry, August 13, 1958; 8 miles N. of Sandpoint, July 8; Robinson Lake, late August, 1958, March 3, May 11, June 1; 3 miles W. of Parma, June 19 (H. W. Homan); Dixie, June 20, 1953 (W. F. Barr), April 17; Fairfield, August 27, 1926 (R. W. Haegele); Gannet, May 22, July 22; Hagerman, May 23, June 20; Bancroft, August 3, 1958; Bear Lake, July 19. MONTANA: Gallatin Co. UTAH: Taylor, Riverdale, Syracuse, Greendale, Corinne, Harper, Far West, Logan, Hooper, Charleston, Garden City, College Ward, Brigham, Ogden. ALBERTA: Edmonton, Wabamun. BRITISH COLUMBIA: Westwick Lake, Kamloops, Quesnel, Nicola.

Hoplodictya spinicornis (Loew).—Fairly common in more permanent marshes in the southern counties of the state. IDAHO: Fruitland, June 8, 1935 (B. F. Coon); 3 miles W. of Parma, June 19 (H. W. Homan); Hot Creek Falls, April 12; Hagerman, April 12. WASHINGTON: O'Sullivan Dam.

Limnia boscii sparsa Loew.—IDAHO: 12 miles N. of Granite, July 8; Elk River, July 4. MONTANA: Glacier Park. Melander (1920) reports this species from Washington.

Limnia costalis brevicostalis Melander.—The type material came from Avon, Idaho (Melander, 1920).

Limnia costalis vittata Melander.—Melander (1920) reports specimens from Montana, Idaho and Washington.

Limnia pubescens (Day).—IDAHO: Moscow, August 8, 1936 (B. F. Coon); Robinson Lake, August 14, September 6, 1958; Lewiston Grade, July 2, 1949 (M. T. James); Kendrick, August 26, 1951 (W. F. Barr). UTAH: Brigham,

Logan. WASHINGTON: Albion, Pullman. OREGON: Portland, Phoenix, Monroe, near Corvallis. ALBERTA: Victoria.

Limnia saratogensis armipes Melander.—The type material came from Olga, Washington (Melander, 1920).

Limnia s. saratogensis (Fitch).—IDAHO: 12 miles N. of Granite, July 8; Gannet, July 22; Fish Haven, July 6, 1951 (G. F. Knowlton). UTAH: Logan, Providence, Salt Lake City, Newton, Lakota, Leeds. WASHINGTON: San Juan Island, Ocean Park. OREGON: Corvallis, Charleston, Spanaway Lake. ALBERTA: Edmonton, Fawcett, Medicine Hat. BRITISH COLUMBIA: Victoria, Chilcotin, Winslow, Kamloops, Goldstream.

Renocera cyathiformis Melander.—IDAHO: 8 miles N. of Sandpoint, June 1, July 8; Elk River, July 4; Stanley Basin, July 22. WASHINGTON: Holotype collected on Orcas Island (Melander, 1920).

Renocera johnsoni Cresson.—IDAHO: Priest River Forest Experiment Station, June 2; Stanley Basin, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); Henry's Lake, July 17. UTAH: Monte Cristo. BRITISH COLUMBIA: Paratype collected at Bear Lake (Cresson, 1920).

Sepedon anchista Steyskal.—Four specimens collected July 19 at Bear Lake constitute the only Idaho records. Steyskal (1956) reports it from Montana.

Sepedon armipes Loew.—Abundant in permanent marshes throughout the state. IDAHO: Priest River Forest Experiment Station, June 2; Bonners Ferry, August 11, 1926 (R. W. Haegele); 8 miles N. of Sandpoint, June 1, July 8; Hauser Lake, May 22 (H. W. Homan); Robinson Lake, September 25; Troy, April 5, 1958; Roswell, July 27 (H. W. Homan); 3 miles W. of Parma, June 19 (H. W. Homan); Bruneau, June 25; Hot Creek Falls, June 27, 1953 (W. F. Barr), April 12; Dixie, June 20, 1953 (W. F. Barr), April 17, June 19; Little Camas Reservoir, June 29 (W. F. Barr); Hagerman, May 23, June 20; Hazelton, September 4, 7, 1954 (W. F. Barr); 4 miles E. of Shoshone, May 22, June 19, July 10; Gannet, May 22, July 22; Stanley Basin, July 22; Salmon, May 25; 2 miles N. of Gilmore, July 24 (H. C. Manis); Massacre Rocks, July 28, 1958 (A. R. Gittins); Bancroft, August 3, 1958. MONTANA: Three Forks, Gallatin Co., Ravalli Co. WYOMING: Jenny Lake in Great Teton National Park. UTAH: Orem, Providence, Brigham, Logan Canyon, Laketown, Ogden, Eden, Mendon, Hooper, Delta, Leeton, Myton, Vernal, Kaneshville, Marysville, Duchesne, Plain City, Lyman, Midvale, Salina Canyon, Spring Run. WASHINGTON: Willow Creek near LaCrosse, O'Sullivan Dam, Coulee. OREGON: Cold Springs, near Prospect, Butte Falls, Minam, 10 miles N. of Seneca, Tumalo Reservoir. ALBERTA: Edmonton, Medicine Hat, Cooking Lake. BRITISH COLUMBIA: Oliver, Kamloops.

Sepedon borealis Steyskal.—Locally common in the more permanent marshes. IDAHO: Priest River Experiment Station, June 2; Dixie, July 31, 1951, April 17 (W. F. Barr), June 19; Gannet, July 22; Stanley Basin, July 22. UTAH: Logan Canyon. OREGON: Corvallis. BRITISH COLUMBIA: Peace River at Fort St. John.

Sepedon fuscipennis Loew.—Abundant in more permanent marshes in northern counties. Not yet recorded from southern and eastern counties where it is apparently replaced by *Sepedon praemiosa*. IDAHO: Kalispel Bay on Priest Lake, July 7; 4 miles S. of Coeur d'Alene, July 14; Granite Lake, June 1; near Westmond, July 8; 3 miles S. of Worley, June 2; Rocky Point on Lake Chatcolet, September 7, 1953 (M. T. James); Robinson Lake, October 12, 1950 (J. K. Vaughn), late August, 1958, May 11; Vassar Meadows, May 6. MONTANA: Ravalli Co. WASHINGTON: Anacortes, Orcas Island, Fort Lewis, Tenino. ORE-

GON: Klamath Falls, 12 miles S. of Corvallis. ALBERTA: Lethbridge, Wabamun, Edmonton. BRITISH COLUMBIA: Agassiz, Haney, Quesnel.

Sepedon lignator Steyskal.—Reported by Steyskal (1959) from Wyoming (Yellowstone Park), Montana (Glacier Park), Alberta (Banff), and British Columbia (Oliver).

Sepedon melanderi Steyskal.—Known only from Snoqualmie Pass, Washington (Steyskal, 1950).

Sepedon neili Steyskal.—IDAHO: Granite Lake, July 2; 3 miles S. of Worley, June 2. Previously this species was known only from the eastern states extending west to Kansas (Steyskal, 1950).

Sepedon praemiosa Giglio-Tos.—Abundant in permanent marshes and in marshy margins of lakes throughout the state. IDAHO: Four miles S. of Coeur d'Alene, July 14; Robinson Lake, October 12, 1950 (J. K. Vaughn), September 6, 1958, May 11; 12 miles S. of Pollock, June 26; 3 miles W. of Parma, June 19 (H. W. Homan); Bruneau, June 25; Dixie, April 17, June 20 (W. F. Barr); Little Camas Reservoir, May 29 (W. F. Barr); Hagerman, April 12, May 23 (R. W. Portman); Rock Creek Ranger Station, Sawtooth National Forest, June 20; 4 miles E. of Shoshone, May 23, June 19; Star Lake, July 4 (D. L. Bishop); Hazelton, August 18, 1954 (A. R. Gittins); Gannet, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); 5 miles N. of Roberts, July 29, 1958 (A. R. Gittins); Bear Lake, July 19. UTAH: Woodscross, Iron Springs, Moab, Harper, Vernal, Green River, Howell, Eureka, Penrose, Logan Canyon, Ogden, Zion Canyon, Randolph, Uinta, Blue Creek, Emery, Syracuse, Hooper, Kamas, Hyde Park, Geneva, Leeds, Brigham, Wellsville, Lehi, Hansville, Amalga, Pahvant. WASHINGTON: Richland, White Bluffs, Pullman, Marietta, O'Sullivan Dam. OREGON: Klamath Co. Fish Hatchery, Cold Springs. ALBERTA: Medicine Hat, Lethbridge.

Sepedon spinipes americana Steyskal.—IDAHO: Bonners Ferry, August 13, 1958; Bear Lake, July 19. UTAH: Wellsville. OREGON: Corvallis. ALBERTA: Wabamun, Fawcett, Clymont.

Tetanocera annae Steyskal.—Not yet discovered in Idaho. BRITISH COLUMBIA: Salmon Arm. Steyskal (1959) records the species from Agassiz, B. C.

Tetanocera ferruginea Fallén.—Berg (1953) reported that the larval stages are predators on aquatic pulmonate snails. In Idaho, a larva was found feeding on a *Lymnaea palustris* snail at the marsh east of Shoshone on May 22. IDAHO: Eleven miles E. of Rogerson, July 20, 1952 (W. F. Barr); Hagerman, May 23; 4 miles E. of Shoshone, May 22, June 19; Gannet, May 22; Mackay, July 7, 1926 (R. W. Haegele); Salmon, May 25; Bancroft, August 3, 1958. UTAH: Salt Lake City, Wellsville. OREGON: Buena Vista, 19 miles N. of Frenchglen. BRITISH COLUMBIA: Prince George, Kamloops, Agassiz.

Tetanocera latifibula Frey (= *hespera* Steyskal).—IDAHO: Dixie, June 19; Stanley Basin, July 22; Swan Lake, July 18; Bear Lake, July 19. UTAH: Pahvant. ALBERTA: Edmonton. BRITISH COLUMBIA: Quesnel, Kamloops, Prospect Lake.

Tetanocera mesopora Steyskal.—IDAHO: Henry's Lake, July 17; Swan Lake, July 18. UTAH: College Ward. ALBERTA: Edmonton.

Tetanocera montana Day.—IDAHO: 10 miles S. of Sandpoint, July 8; Swan Lake, July 18. MONTANA: Fortine. ALBERTA: Tofield, Wabamun, Nordegg, Banff. BRITISH COLUMBIA: Kamloops.

Tetanocera nanciae Brimley.—Abundant in marshes and swales throughout the state. IDAHO: Westmond, July 8; Robinson Lake, September 15, 1958, June

10; Laird Park, June 24, 1949 (M. T. James); Kendrick, August 26, 1951 (W. F. Barr); Elk River, July 4; 12 miles S. of Pollock, May 30; Hot Creek Falls, July 12, 1952 (W. F. Barr); Bruneau, June 25; Dixie, June 20, 1953 (W. F. Barr), June 19; Rock Creek Ranger Station, Sawtooth National Forest, July 19, 1952 (W. F. Barr); 4 miles E. of Shoshone, May 22, June 19, June 29 (D. L. Bishop); Dietrich, July 9 (D. L. Bishop); Gannet, July 22; Stanley, August 6, 1950 (R. W. Portman); Challis, June 23, 1952 (E. I. Schlinger); near Mackay, July 30, 1958 (A. R. Gittins); 2 miles N. of Gilmore, July 24 (H. C. Manis); Arco, August 8, 1958; Massacre Rocks, July 28, 1958; Kilgore, July 15, 1956 (W. F. Barr); Henry's Lake, July 17; Sugar City, August 10, 1940 (W. E. Shull); near Aberdeen, July 8, 1957 (A. R. Gittins); Wayan, July 16, 1940 (W. E. Shull); Montpelier, July, 1951 (G. F. Knowlton). MONTANA: Lewistown, Sahara, Fortine. WYOMING: Yellowstone Park, Sheridan. UTAH: Logan, Kamas, Devil's Kitchen, Hyde Park, Marysvale, Laketown, Woodruff, Eden, Wahship, Payson, Mantua, Vernal, Promontory, Fairview, Garden City, Linden, Smithfield, Hooper, Plain City. WASHINGTON: Ocean Park, Pullman, N. Yakima, Johnson, Rainier National Forest, O'Sullivan Dam, Grand Coulee, near Spanaway, Spanaway Lake, Fort Lewis. OREGON: Klamath Falls, Minam, Redmond, near Prospect, Enterprise, 20 miles S. of Bend, Powell Butte, Tumalo Reservoir, 10 miles NE. of LaPine. ALBERTA: George Creek, Nordegg, Banff, Wabamun, Edmonton, Pincher, Cypress Hills, Medicine Hat. BRITISH COLUMBIA: Jesse Island, Kamloops, Quesnel, Vernon, Nicola, Smithers, Chilcotin, Agassiz, Prospect Lake.

Tetanocera nigricosta Rondani.—Not yet discovered in Idaho. ALBERTA: Edmonton, Fawcett, Wabamun, Wetaskiwin, Gull Lake. Melander (1920) records the species from Mt. Constitution, Washington.

Tetanocera obtusifibula Melander.—IDAHO: Near Moscow, May 30. Melander (1920) had type material from Worley, Idaho. WASHINGTON: Pullman. Chambers. OREGON: Nine miles N. of Brownsville, slough 10 miles S. of Corvallis.

Tetanocera oxia Steyskal.—Not yet discovered in Idaho. MONTANA: Three Forks. Steyskal (1959) records the species from Fawcett, Alberta.

Tetanocera plebeia Loew.—Fairly common, but local, in both permanent and vernal marshes throughout the state. IDAHO: Kalispel Bay on Priest Lake, July 7; 8 miles N. of Sandpoint, July 8; Westmond, July 8; Robinson Lake, September 10, 1958; Elk River, July 4; 12 miles S. of Pollock, May 10, June 26; Dixie, June 19; Stanley Basin, July 22; 4 miles E. of Shoshone, June 19; Declo, September 14, 1930 (F. Gillett). WYOMING: Yellowstone Park. UTAH: Newton. Henefore, Woodruff, Mt. Home, Logan, Kanab, Mt. Nebo. WASHINGTON: Walla Walla, Ilwaco. OREGON: Enterprise, near Prospect, Summit Prairie, Odell Lake, near Sisters. ALBERTA: Nordegg, Banff, Edmonton.

Tetanocera robusta Loew.—Abundant in the more permanent marshes throughout the state. IDAHO: Priest River Forest Experiment Station, June 1, Bonners Ferry, August 13, 1958; 8 miles N. of Sandpoint, June 1, July 8; Robinson Lake, late August, 1958; Kendrick, September 25; Spaulding, May 17, 1954 (W. F. Barr); Bruneau, June 25; Little Camas Reservoir, May 29 (W. F. Barr); Hagerman, June 20; 4 miles E. of Shoshone, June 29 (D. L. Bishop); Declo, September 14, 1930 (J. Gillett); Elba-Basin Pass, June 22; Stanley Basin, July 22; Hailey, July 28, 1956 (R. W. Portman); 2 miles N. of Gilmore, July 24 (H. C. Manis); Sugar City, July 21, 1926 (R. W. Haegele); Bancroft, August 3, 1958; Fish Haven, July 6, 1951 (G. F. Knowlton). MONTANA: Hamilton Phillipsburg. UTAH: Newton, Midway, Benson, Heber, Logan, Hyrum, Milford, Lehi, Pahvant, Wallsburg, Wellsville, Randolph, Hooper, Valencia,

Plain City, Ogden. WASHINGTON: Pullman, Harrah, Ocean Park, Custer, Prosser. OREGON: Klamath Falls, Pringle Falls, Enterprise, Blue Mt. Hot Springs, 10 miles S. of Corvallis, Swim, near Strawberry Lake. ALBERTA: Nordegg, Winterburn, Gull Lake, Medicine Hat, Calgary. BRITISH COLUMBIA: Soda Creek, Kamloops.

Tetanocera rotundicornis Loew.—Berg (1953) reared adults from larvae found in the land snail *Oxyloma decampi gouldi*. In Idaho, the species was found only in those marshes containing large populations of *Oxyloma*. IDAHO: Eight miles N. of Sandpoint, July 8; Dixie, June 19; 4 miles E. of Shoshone, June 19, June 29 (D. L. Bishop); Gannet, July 22. OREGON: Klamath Falls. ALBERTA: Wabamun, Fawcett. BRITISH COLUMBIA: Chilcotin, Kamloops.

Tetanocera soror Melander.—IDAHO: Westmond, July 8; Moscow Mt., July 24, 1936 (B. F. Coon); Robinson Lake, August 14, September 6, 1958; Dixie, June 19. WASHINGTON: Chambers, Pullman, Orcas Island. OREGON: Summit Prairie, 10 miles S. of Corvallis, Corvallis.

Tetanocera silvatica Meigen.—Not yet discovered in Idaho. ALBERTA: Gull Lake, Wabamun, Mt. Athabasca. BRITISH COLUMBIA: Peace River at Fort St. John.

Tetanocera spirifera Melander.—Not yet discovered in Idaho. WYOMING: Jenny Lake in Great Teton National Park. Steyskal (1959) records the species from Alberta (Banff National Park) and British Columbia (Atlin).

Tetanocera unicolor Loew.—IDAHO: Bonners Ferry, August 11, 1926 (R. W. Haegele); 8 miles N. of Sandpoint, June 1, July 8; Gannet, July 22; Stanley Basin, July 22. MONTANA: Three Forks.

Tetanocera valida Loew.—Not yet discovered in Idaho. UTAH: Logan. ALBERTA: Edmonton, Vermillion, Medicine Hat, Gorge Creek. BRITISH COLUMBIA: Chilcotin.

Tetanocera vicina Macquart.—IDAHO: Eight miles N. of Sandpoint, July 8; Rocky Point on Lake Chatcolet, July 1, 1953 (M. T. James); Robinson Lake, October 1, 1958; Elk River, July 4; 3 miles W. of Parma, June 19 (H. W. Homan); Dixie, June 19; Bear Creek Camp, 10 miles N. of Leslie, July 10, 1956 (W. F. Barr); Henry's Lake, July 17. WYOMING: Yellowstone Park. UTAH: Miner's Peak. WASHINGTON: Ocean Park, Marietta, Pullman, Orcas Island. OREGON: Butte Falls, Sheep Creek, Minam, Corvallis, near Prospect, north of LaPine.

Trypetoptera canadensis (Macquart).—Not yet discovered in Idaho. MONTANA: Sahara. UTAH: Logan, Wellsville, Nible, Brigham, Ogden, Smithfield. BRITISH COLUMBIA: Langley, Jesse Island, Saanich District, Victoria.

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Investigations in the Life History of the Common Coturnix

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ABSTRACT: A compilation of the known life history data of *Coturnix coturnix* is presented. Topics include description of juvenal and adult plumage, weights and linear measurements. Voice, habitat and distribution are considered as well as aspects of reproduction. Decimating factors, rate of survival, food and behavior are also considered.

INTRODUCTION

The purpose of this paper is to summarize present knowledge concerning the life history of the quail *Coturnix coturnix*. The summary is based on a review of literature and on personal experience of the investigator in the laboratory and game farm. *C. coturnix* is a small, chubby, tailless, cinnamon-colored, terrestrial galliform introduced into North America from Japan during the late 1950's. It is 7 to 8½ inches in length. *Coturnix* now found in North America were stocked from game-farm propagated flocks of the subspecies *C. coturnix japonica*. It is extremely variable and adaptable in many aspects of its biology; probably an evolutionarily unstablized form with many accelerated and merostatic growth characters (Wetherbee, 1959a).

DESCRIPTION

ADULT MALE

NUPTIAL PLUMAGE

Head.—Median stripe and superciliary line white; forehead, crown and nape black edged with brownish red; bill galliform but not robust, blackish brown to black, iris buffy brown ("yellow in old male birds," Montagu, 1831, probably in error); face and throat light brownish red. Nostrils slit-like, covered by an oblong operculum. Chin and throat with rounded feathers variable in tone, brownish red, perhaps darker brownish red with age, sometimes with black "anchor" mark (typical of the nominate race) consisting of blackish brown band descending from ear-coverts and terminating in throat patch; apparently most common after the second year.

Upper parts.—Large cinnamon feathers with few pale gray bars edged with black and with broad medial cream stripes.

Under parts.—Light cinnamon to light gray. Large pointed feathers of flank confluent with those of breast with white median stripe bordered by broad black and rufous edges.

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² A contribution from the Federal-Aid to Wildlife Restoration Program, Surveys and Investigations Project, Nebraska W-30-R.

Tail.—Small, mostly concealed by coverts; rectrices 10 - 12 (Coues, 1903), coverts only 8 (Clark, 1918). Striped buffy brown, black and cream. Cloacal region swollen and reddish.

Wings.—Pointed due to long, curved tenth primary. Primary 10 as long or longer than 9 and emarginated on inner web; 9 and 8 emarginated on outer webs. Olive with about ten irregular cinnamon bars on outer webs of remiges; tertials buffy brown with several narrow pale gray bars edged with black. Greater coverts olive; lesser coverts brownish olive. Undersurface light gray; lesser under coverts white tinged with cinnamon.

Legs and feet.—Buffy yellow; without spurs; hind toe elevated,

Adult postnuptial molt.—Complete, extremely variable in time; June to January (Dementev and Gladkov, 1952), but usually in August (Witherby *et al.*, 1941); often absent in domestic stock (Kuroda, 1924). Stejneger (1885) reports shedding of claws; but this is probably pathological.

NON-NUPTIAL PLUMAGE

Feathers on chin and sides of throat long and lanceolate, generally whitish. Feathers on the lower parts rounded; some have blackish brown mark on medial throat suggesting "anchor" mark of nominate form (Kuroda, 1924). Juvenal distal primaries, retained in first non-nuptial plumage, have small sharp tips and coverts usually without white rachises; blunt primaries on second year birds and coverts usually with white rachises (David Lyon, personal communication). These covert markings are the reverse of age criteria for the Bob-white (*Colinus virginianus*).

Pre-nuptial molt.—Contour feathers only, partial; February to April (Dementev and Gladkov, 1952), occasionally to May (Witherby *et al.*, 1941), especially for throat and flanks (Kuroda, 1924).

ADULT FEMALE

NUPTIAL PLUMAGE

Like male except feathers on chin and sides of throat long and pointed, much lighter cinnamon, usually margined on outer or both webs with rufous or black spots near tip without black median band. Postnuptial molt as in male.

NON-NUPTIAL PLUMAGE

As in nuptial plumage, pre-nuptial molt probably as in male.

COLOR PHASES

Albinism has been reported in females at the rate of "one in 70,000"; the eyes were pink and the feathers of the back and sides showed markings due to structure rather than pigment (Wint, 1957). "Blue" eyes were reported in albinos by Hachisuka (1931) who also reported that albinos lay white or pale bluish eggs with bluish markings. Shimakura (1940) described a simple, Mendelian, autosomal

recessive plumage character, "brown-splashed white." Incomplete melanism is reported by Dementev and Gladkov (1952); complete melanism, by Sturniolo (1913).

NATAL PLUMAGE

Relatively more dusky and striped than North American galliforms. Head tawny with black spot above culmen; medial stripe buffy brown bordered by black stripes; auricular patch black. Back and wings buffy brown with four blackish brown stripes on dorsum; tail and anterior border of wing blackish brown.

Natal down lost by abrasion; loss starts at 4 days and is completed last on head at about one month.

FIRST JUVENAL PLUMAGE

A few primaries are visible at hatching; all 10 are functional at 11 days at which time the chick can fly short distances. Ventral, femoral and humeral are visible at 4 days; capital, at 9 days. Plumage complete at 25 to 30 days (David Lyon, personal communication) except that primaries 9 and 10 are still sheathed at 21 and 42 days but clean at 7 weeks (Dementev and Gladkov, 1952). This plumage appears as adult female plumage except the cream medial streaks of spinal feathers are narrower and unsymmetrical (David Lyon, personal communication). Bill light brownish black.

First postjuvinal molt.—Contour feathers only, probably partial; breast, back and femoral feathers at 20 days of age to 50 days (David Lyon, personal communication), 26 to 42 days (Heinroth and Heinroth, 1928). Remiges: secondaries, centripetal, complete; primaries, centrifugal, incomplete (Dementev and Gladkov, 1952). First primary drops at 21 to 25 days; second, 22 to 27; third, 27 to 33; fourth, 33 to 36 (Edwards, ms.), 42 days (Dementev and Gladkov, 1952). David Lyon (personal communication) recorded first primary dropped at 22 to 29 days; second, 23 to 34; third, 27 to 39; fourth, 34 to 50; fifth, 34 to 75; sixth, 40 to 82, and seventh, 49 to 96 days. Wing molt becomes irregular and stops at sexual maturation (neoteny) which is variable in onset from loss of fourth primary to loss of seventh or eighth primary (6 to 14 weeks).

SECOND JUVENAL PLUMAGE

Spinal feathers appear at 20 days, their light medial streaks are broad as in adult (David Lyon, personal communication). Sexes as in adult plumage with cinnamon on breast of male and female with speckled breast; a minority of specimens may not show sex dimorphism of plumage until first non-nuptial plumage (David Lyon, personal communication). The birds migrate with retained distal juvenal primaries.

Second post-juvinal molt.—Contour feathers only, complete at 11 to 13 weeks of age for July-hatched birds, 8 to 10 weeks for September-hatched birds (David Lyon, personal communication). Ac-

quisition of first non-nuptial plumage is accelerated for birds hatched late in the season, and as probably determined by photo-period of first half of October. Heinroth and Heinroth (1928) recorded 14 to 18 weeks, Stanford (1957), 20 to 22 weeks for this acquisition.

LINEAR MEASUREMENTS

Adult wing 91 - 104 mm, culmen 11.5 - 14.5 mm, tail 31-43 mm, tarsus 23.5 - 30.5 mm (120 from Japan, Kuroda, 1924); average wing 96 mm (27 from U.S.S.R., *C. c. japonica*, Dementev and Gladkov, 1952); body length 175 - 215 mm, wing-span 327 - 390 mm (34 from U.S.S.R., *C. c. coturnix*, Dementev and Gladkov, 1952); tarsus 17 mm at one week, 28 mm (maturation) at two weeks (David Lyon, personal communication). There is no sexual dimorphism in lengths.

WEIGHT

Neonatal 7.0 - 8.9 gms, average 8.0 gms (6 domestic, Wetherbee, 1959a); 5-6 gms (feral, Uljanin, 1941); 5 gms at 0 days, 10 gms at 4 days, 20.5 gms at 8 days, 41 gms at 16 days, 97 gms at 35 days, 120 gms at 49 days (Heinroth and Heinroth, 1928); average adult 87.6 - 90.5 gms, may reach 146 gms by fall migration (*C. c. coturnix*, Dementev and Gladkov, 1952); without sex dimorphism in weight except that females kept in captivity are much heavier than males. The quail may double its weight in autumn in conjunction with physiological *zugdisposition*, indeed the Arabic names of this bird, *Salwa* and *Summaneh* mean "to be fat" (Jones, n.d.; Wyatt, 1870).

SUBSPECIES

Coturnix coturnix africana Temminck and Schlegel 1849 is a darker, smaller race with rufous sides of head. It replaces *C. c. japonica* Temminck and Schlegel 1849 in Africa. *C. c. coturnix* (Linne 1758), larger and with black anchor band on throat and with rounded feathers on chin and throat in all plumages, replaces these races in western Asia and Europe. The nominal race was stocked unsuccessfully in North America in the nineteenth century. Recognized insular races include *C. c. conturbans* Hartert 1917 on the Azores; *confisa* Hartert 1917 on Madeira and *inopinata* Hartert 1917 on Cape Verde. The races *ussuriensis* Bogdanov 1884 of central Asia and *erlangeri* Zedlitz 1912 of Ethiopia are of doubtful validity.

FIELD IDENTIFICATION

The Common Coturnix is a cinnamon, striped galliform that runs rapidly and is smaller than the Bobwhite. Its flight is rapid, straight and low with quick wing beats and after a short distance the bird glides to the ground. Unlike the Bobwhite, they are seldom flushed in more than pairs.

The castenet-like crowing of the male, "pick-per-a-wick" with a gurgle in the middle, is distinctive. The droppings of males, with froth adhering, are sometimes diagnostic signs. The relatively broad

stripes of the spinal feathers distinguish adults from juvenals under 20 days of age. It does not perch in trees.

VOICE

A loud castanet-like crow, variably accented, "pick-per-a-wick" or "ko-turr-neex" is given by the male. This call has a brief pause between each clearly defined note and is repeated several times with a few seconds' interval between calls (Stillwell and Smith, 1880). Crowing is usually associated with the absence of a female (Moreau, 1951); it is rendered from mid-March to August (Dementev and Gladkov, 1952) and is resumed briefly in September (Jacobs, ms.), probably in association with autumnal recrudescence of the testes. The initial call occurs at five or six weeks of age. Coturnix crow during the night from 9 PM to 7 AM during the height of breeding season (Pfeifer, 1954); more pronouncedly before sunrise. In cloudy weather they crow throughout the day but are quiet during rain (Schwartz and Schwartz, 1949). In captivity they are reputed to be quiet in a lighted room but crow when the room is darkened (Montagu, 1831). The call is heard up to 200 feet (Edwards, ms.) or one-half mile (Moreau, 1951). The bird crows in an open place with neck raised, eyes shut, head on one side, and body raised at full height (Montagu, 1831); the body sinks down during the act. Historically, Japanese birds were selectively bred to trill at the end of the crow (Meise, 1954).

"Brr-up, brr-up, brr-up" ("braw-wow," close by), a subdued, hoarse, vibrating, ventriloquial call is given by both sexes (Pickford, 1945) and is said to be a mutual invitation to copulate (Naumann, 1905).

"Peu-peu" is a call given by the female, timed to coincide with the first and last syllables of the male's crow (Campbell, 1952).

Pickford (1945) records the alarm note as "pap, ata, pap-pap-pap-pap-pap." When flushed some Common Coturnix give a soft plaintive note like that of the Pectoral Sandpiper (*Erolia melanotos*) (Stillwell and Smith, 1880). The call of the very young is also disyllabic and like that of a sandpiper.

A high, cricket-like noise, "weet-weet, weet-weet" is sometimes given by the adult much like the call of the guinea fowl (*Numida pucherani*).

Ruthke (1933) records instances of calling in flight at night.

Descriptions and figures of quail-pipes used to imitate the call are given in the Encyclopaedia Britannica of 1797 (Moreau, 1951); in Rowley's Ornithological Miscellany (Newton, 1893-96); by Witherby (1903); and by Campbell (1952).

HABITAT

General.—Agricultural fields and upland grassland, especially wheat and clover, are favored. It avoids very tall and dense vegetation (Witherby *et al.*, 1941) and mountains and marshes (Jones, n.d.). Habitat is much localized and occupied variably each year.

Special.—The Common Coturnix prefers breeding areas and nesting habitat of wheat, oats, barley (Moreau, 1951), alfalfa more than six inches high (Jacobs, ms.), or clover (Westerskov, 1947). (Note: "Corn" of Old World authors is "grain," most often "wheat" in American usage, not maize). In the Canary Islands, Cullen *et al.*, (1952) found this species in open mixed forest. Migration and winter range habitat is characterized by root fields in England (Witherby *et al.* 1941), crops or short grass in Arabia (Meinertzhagen, 1954), steppes (Jones, n.d.) and heath (Cullen *et al.*, 1952).

The feeding habitat is strictly limited to the ground along peripheries of dense vegetation (Schwartz and Schwartz, 1949). In Africa, Cheesman and Sclater (1935) found them feeding in fields of dwarf millet. Roosting habitat is in the heavier marginal grass (Schwartz and Schwartz, 1949). Resting habitat is in small barren openings (Schwartz and Schwartz, *op. cit.*) where the birds often dust bathe. For refuge habitat it favors grass (Schwartz and Schwartz, *op. cit.*) or shelter under a bush or rock in flat desert (Meinertzhagen, 1954). As fields are mowed the birds leave because of the loss of standing cover (Jacobs, ms.).

DISTRIBUTION

Coturnix coturnix is found on all the Old World continents. It is migratory. Its distribution is strongly influenced by agriculture (Westerskov, 1947). In North America it has been introduced in three general stages as follows:

Stage 1.—Several thousand captured birds (*C. c. coturnix*) were imported from Sicily in 1877-1882, mostly under the auspices of M. G. Everts and W. Hapgood and released in the Northeast (100 as far west as Sioux City, Iowa; Tobey, 1882). These early introductions were made under the names of European, Egyptian, Messina (not "Massena Quail," *Cyrtonyx montezumae*), and Migratory Quail and were contemporaneously chronicled in *Forest and Stream*. (For bibliography see Phillips, 1928). Some of the introduced birds migrated south as far as Georgia; many reputedly returned and bred three years in succession (for bibliography see McAtee, 1944). The experiment was conceded a failure by 1885.

Stage 2.—Restaurants on the West Coast imported many thousand live *C. c. japonica* as "Migratory Chinese Quail" from 1895 to 1904; many of these escaped or were confiscated and released. Deliberate small plantings were made in the state of Washington in 1923; none survived the first year (Grinnell and Miller, 1944; Phillips, 1928).

Stage 3.—Several hundred thousand game-farm propagated Common Coturnix were stocked simultaneously as "coturnix" or "stubble" quail during the late 1950's in most of the southeastern and south-central states by the game commissions of these states in accord with a plan conceived by M. O. Steen. All or most of these birds descended from 140 breeders of the Missouri Conservation Commission and

were imported by J. W. Steinbeck of Concord, California, from Japan in 1953. Commercial propagators probably also used this same basic stock. Some of the released birds bred (an average of 62 yards from release sites in Oklahoma; Jacobs, ms.) and migrated to southern United States the year of release.

The *coturnix* race was unsuccessfully reintroduced in Ireland (Ussher and Warren, 1900); but the *japonica* race was successfully introduced in Hawaii in 1921 (Schwartz and Schwartz, 1949).

MIGRATION

The patterns of migration of this species are probably not standardized even in the Old World (Moreau, 1951). Adult males and females may migrate separately according to Alexander (1898), while Ulianin (1941) recorded that females migrate with their young. The migration flights occur at night. Moreau (1953b) gives a record of this species migrating at 57 miles per hour. Conflicting data on wind directions supposedly conducive to migration are summarized by Moreau (1953a). The Common Coturnix flies 10 to 20 feet high during migration and in compact groups of 12 to 30 birds (Meinertzhagen, 1920) or even larger (Taka-Tsukasa, 1935) although Elliott and Monk (1952) record only two or three individuals passing per minute. They separate by day (Meinertzhagen, 1954). The same author curiously records that these flights of Common Coturnix are "often accompanied by a single land rail." This is also mentioned by Pliny (Rackham, 1940) of antiquity.

Many quail perish over the sea (Gurney, 1901; Moreau, 1928), hit lighthouses (Meinertzhagen, 1924) and perch on vessels (Rackham, 1940) before arriving at their destinations. Wood (1945) records this species alighting momentarily safely on the sea. In Palestine, Meinertzhagen (1920) records the bulk of the migrants resuming their journey the evening subsequent to arrival in fall.

In the Old World a few winter in northern latitudes, i.e. England (Jones, n.d.); most arrive in Denmark in early May and leave in October; Northern Scandinavian coturnix pass through Denmark as late as the first two weeks of November (Westerakov, 1947). At Port Said, Egypt, they are found during the second week of September (Meinertzhagen, 1954). In England they arrive in March and April and leave near the end of September (Newton, 1893-96).

Interseasonal movements (*zwischenzug*) across the Mediterranean Sea of both young and old birds occur (Moreau, 1951). Migration restlessness (*zungunruhe*) is described as occurring at seven weeks of age by Heinroth and Heinroth (1928) and at six weeks by Meise (1954).

North American band recoveries show direct southerly autumnal migration of birds released in spring, summer and fall. Released birds may breed on the site or disperse several miles. Six of thirty recoveries of Common Coturnix released in Nebraska during 1957 were taken in Texas. One released in Bourbon, Kentucky, on July 9,

1957, was recovered in Saginaw, Michigan, about 107 days later (Stephens, ms.).

One bird released July 17, 1957, in Nance County, Nebraska, was recovered alive, March 11, 1958, in Hall County, Nebraska. Since six other birds of this release group were taken during the winter in Oklahoma and Texas and, since there was an absence of winter records substantiated by specimens in Nebraska, the above recovery is probably evidence of return migration.

BANDING STATUS

Banding of *C. coturnix* is administered by individual states; there is no central organization for collection of data. A representative instance is Nebraska where 23,740 were banded and released during the summer of 1957. There were 18 recoveries the following winter, all directly south in Kansas, Oklahoma and Texas. In Japan, Austin and Kuroda (1953) reported a similarly low per cent (8) recovered of 12,554 banded over twelve years. In Italy (Toschi, 1956) one per cent were recovered of one-half million banded and released on hunting areas. In France, 2.6 per cent of 2000 released were recovered within five months (Glegg, 1941).

REPRODUCTION

AGE AT MATURATION

The Common Coturnix is capable of breeding in the same year that they are hatched. Under domestication, females lay fertile eggs as early as 31 days of age and males mature sexually at 28 days (Wetherbee, 1959b). A released female that was hatched April 28 established a feral nest at 67 days of age (Edwards, ms.). The October nesting reported on Cape Verde Islands by Bourne (1955) was possibly by a bird of the year. The usual breeding is late in May and in June in England and is correlated with growth of tall grass crops (Lack, 1950).

TERRITORY

Breeding territory is advertised from a crowing ground, usually a slightly elevated spot in a clearing and bare except for a clump of vegetation. The male normally crows in the shadow of the clump. In Hawaii these crowing grounds are usually about 100 yards apart in densely populated areas, indicating the general size of territories (Schwartz and Schwartz, 1949).

PAIR-BOND

Claims of polygamy by authors (Dementev and Gladkov, 1952) are probably unsubstantiated and stem from observations of domestic birds. The Common Coturnix is probably seasonally monogamous (Coward, 1926; Moreau, 1951), except when a local surplus of females makes polygamy possible (Naumann, 1905). A description of the mating dance of the male by Pfeifer (1954) indicates that

the male jumps up and down excitedly, higher and higher to three to four feet for about one minute. It is then heard to give a nasal "wuar-wuar-wuar" while its wings are slightly elevated; the female is inattentive. The courtship is described by Bailey (1854). The male runs quickly to the female, stops along side her and keeps turning round her, dragging his wings, and stretching his neck with the feathers of his throat and breast puffed out.

Crowing by the male seems to be dependent upon the absence of the female; mated males call little (Moreau, 1951). Dementev and Gladkov (1952) indicate that the male follows the cry of the female. There is probably a mutual maintenance of the pair-bond stimulated by calling. Both male and female quail-pipes are used with success by pot hunters. In the breeding season in South Africa, Roberts (1940) noted that they often spring up in pairs, fly parallel for a time and then cross over.

COPULATION

Under domestication these birds are actively promiscuous throughout the year; females lose their spinal and cervical feathers from repeated treading by the male. The female is usually bitten on the nape during copulation. Pfeifer (1954) describes the rape of a wounded female Common Coturnix by the male. The English word, "quail" has as one of its meanings; a courtesan, in allusion to the amour of this species. When released during stocking operations, the birds often copulate on the spot before dispersing. Cross-breeding experiments (Jones, n.d.; notwithstanding) with Bobwhite *Colinus virginianus* (1500 eggs) all gave negative results (Stanford, 1957).

Male *C. coturnix* have a penis with pigmented base on the ventral cloaca. Its cloaca is usually filled with a meringue-like substance, probably secreted by a large gland on the dorsal wall of the cloaca. The histochemistry and histology of the cloacal gland and penis is described by Coil and Wetherbee (1959). The cloacal substance probably acts as an analog to secretions of the mammalian Cowper's gland, aiding in sperm transfer. The secretion adhering to the droppings cause the feet of caged birds to accumulate large balls of dung.

The testes of a sexually mature male coturnix average 15×25 mm.

NEST

The nest is well concealed in grassy cover (Schwartz and Schwartz, 1949) and looks like the nest of the Ring-necked Pheasant (*Phasianus colchicus*) but it is smaller. Outside diameter is 6 to 7 inches; inside diameter, $3\frac{1}{2}$ to $4\frac{1}{4}$ inches; inside depth, 1 to 2 inches. It is constructed of dried weeds, leaves and stems placed around a shallow depression in the ground, without a canopy (Edwards, ms.). Nest building is done by the female only (Schwartz and Schwartz, 1949). Some nest are well-woven to a thickness of 1.5 cm (Uljanin, 1941) and sometimes lined with feathers (Dementev and Gladkov, 1952).

or duff but without cementing material (Edwards ms.). Most of the building is accomplished between the laying of the first and fifth eggs; none during incubation (Edwards, ms.).

EGGS

The first viable eggs are laid in early May. There is mass laying in middle May in the Chkalovskii District of U.S.S.R. and in June in the Krasnoyarsk District (Dementev and Gladkov, 1952). In Denmark forty-four per cent of the nests were found in August. Many records of eggs in September (example pictured by Westerskov, 1947) listed by Dementev and Gladkov, (1952) may be of eggs laid by birds of the year. In captivity the Common Coturnix lays throughout the year: 200 eggs per year (Cott, 1953), 250 per year (Austin and Kuroda, 1953), 365 per year (Meise, 1954).

Clutch size.—There are 6 or 7 eggs laid per clutch in Equatorial and South Africa, 6 to 8 in India, and 8 to 12 in Europe with an increase from west to east in Europe (Lack, 1947); ten is the usual number in England (Lack, 1948). In a study made in Denmark, there were 8 to 15 eggs per clutch with an average of 10.2 eggs in 17 clutches (Westerskov, 1947). In North America, Edwards (ms.) found that birds released in Ohio laid 5 to 13 eggs per clutch with an average of 8.6 eggs. He found a single replacement clutch with 7 eggs. Clutches of 17 to 20 eggs have been reported (Everts, 1878; Montagu, 1831; Dementev and Gladkov, 1952). Since individual females may lay eggs of varied shape and color, mixed clutches cannot be distinguished by these criteria. Late clutches were not found to be smaller than early ones by Westerskov (1947).

Shape.—While, in general, the eggs of this quail are of a short oval shape, they vary toward pyriform even in single clutches. Their shell texture is hard, smooth and glossy but often with a white bloom. The ground color is a light buffy yellow with chestnut to black speckles, spots and blotches, variable in extent even within single clutches. Spots can be rubbed off with the fingernail. The viteline membrane is exceedingly tough and the eggs cannot be candled by the use of simple techniques.

Size.—The average of 100 eggs from U.S.S.R. was 29.41×22.79 mm with maxima of 25 and 32 mm and minima of 21 and 25 mm; one clutch of 15 eggs averaged 29×23 mm, and had maxima of 28 and 31 mm and minima of 22 and 24 mm (Dementev and Gladkov, 1952). The average of 100 British eggs was 30.37×22.99 mm with maxima of 32.7×23.6 mm and 30.2×24.9 mm; and minima of 27.9×22.0 and 29.6×21.2 mm (Witherby *et al.*, 1941). In South Africa, Roberts (1940) recorded averages of 20.0 to 30.3 mm $\times$ 21.7 to 24.4 mm; in Denmark, Westerskov (1947) recorded the average of 26 eggs, 26.1 to 31.5 mm $\times$ 20.6 to 23.2 mm; and in Japan, Austin and Kuroda (1953) recorded averages of 28.8×22.4 mm.

The weight of fresh eggs in Germany was reported by Heinroth

and Heinroth (1928) to be 8 to 9 gms; the yolk, 3.2 gms or 35.5 per cent of the total weight. In Russia, Uljanin (1941) weighed eggs at 5.6 to 7.0 gms, two days before hatching. Eggs produced under domestication are relatively larger than those in the wild, and 10 to 15 grams is not unusual.

EGG DEPOSITION AND REPLACEMENT

The Common Coturnix lays one egg daily (Uljanin, 1941). Edwards (ms.), in field-pen studies, found no dump nests as in pheasants. The same investigator found that a clutch of 9 eggs that had been incubated 10 days was replaced 10 days after being disrupted; and a clutch of 6 eggs that had been incubated 6 days was replaced by 7 incubated eggs 11 days after the date of disruption. A clutch of 26 eggs was thought by Witherby *et al.* (1941) to be laid by two females. Laying birds deposit large fecal droppings.

Incubation attentiveness.—Incubation begins on completion of the clutch (Witherby *et al.*, 1941) and is performed by the female only. She has an incubation patch (Austin and Kuroda, 1953; Edwards, ms.; Dementev and Gladkov, 1952). The latter authors record the unusual occurrence of two different males (sex determined by dissection) incubating in Russia and with well-developed incubation patches. The female does not flush easily (Whitehead, 1909) and is often killed on the nest. Edwards (ms.) found that the sitting bird can be lifted off the eggs with subsequent desertion; however, it does desert if the nest or eggs are damaged. The hen was not known to share incubation with others in Edwards' study. Large clutches of eggs were said to be layered during incubation (Stillwell and Smith, 1880).

Incubation period.—The average minimum time required for



Fig. 1.—Sternum, coracoid, furculum and ventral ribs of just-hatched *Coturnix coturnix* (left) and *Lophortyx californicus* (right) compared. Although the former hatches in only sixteen days and latter in twenty-three days, the bones of the former are much further ossified at hatching. A striking feature of the life history of *C. coturnix* is its accelerated ontogeny.

hatching of 100 commercial eggs was 395 hours (16.4 days) with a range from 380 to 432 hours under artificial incubation of 99.5°F. dry bulb, 89°F. wet bulb, forced draft (Wetherbee, 1959b). Heinroth and Heinroth reported incubation periods of 16 and 17 days (1928). The body temperature of 110°F. of the Bobwhite (*Colinus virginianus*) was found to be the same for *Coturnix coturnix* by Jacobs (ms.) in spite of 7 days' difference between these two species in incubation period. Furthermore, Wetherbee (1959) found that newly-hatched *C. coturnix* exceed Bobwhite and other quails in extent of ossification in spite of the difference of a week in incubation periods. (See Figure 1.) Line drawings of embryos for each of the 16 days of incubation were made by Edwards (ms.). There is a two-day interval between the hatching of the first and last chick of the brood according to Dementev and Gladkov (1952) and Jacobs (ms.). The brooding hen readily adopts fostered offspring (Jones, n.d.).

Flightless period.—The young leave the nest a few hours after hatching and are brooded by the female only (Heinroth and Heinroth, 1928). They disperse as far as 100 meters four days after hatching (Dementev and Gladkov, 1952). Broods average five young in Hawaii (Schwartz and Schwartz, 1949). Weight of newly hatched young is about 8 grams. The temperature-regulatory mechanism is not fully developed at hatching; homiothermy was not found in the tested range of 28 to 37°C. by Boni (1942). The young fly short distances at 11 days of age and fly strongly at 19 days (Heinroth and Heinroth, 1928).

Number of broods per year.—There are conflicting evidences regarding the number of broods produced per year. Uljanin (1941) is dogmatic in stating that this species is single-brooded in all latitudes of U.S.S.R. Records of multiple broods are attributed to replacement clutches, to variability of reproductive readiness of the female (Dementev and Gladkov, 1952) and to birds of the year perhaps breeding in the fall since they mature sexually under domestication in 4 weeks. The Common Coturnix is reputed by Berthet (1949) to reproduce in Africa during the winter and again the same year in Europe after migration.

SURVIVAL

Rate of survival.—In Japan, 1007 recoveries from 12,554 banded Common Coturnix in the period 1925 to 1937 show a shooting toll of only 8 per cent, which is low for a game species. As 89.4 per cent of the recoveries were taken within the first year after banding, 9.3 per cent, the second year, and only 1.2 per cent survived into the third year, an average annual mortality of about 90 per cent is indicated and it follows that there is a population turnover of practical completeness every two years (Austin and Kuroda, 1953). The potential life span of individuals would be expected to be brief considering the acceleration of other aspects of the birds' development.

There are great fluctuations in population levels and the species may well be "cyclic" on the Cape Verde Islands (Bourne, 1955). Westerskov (1947) correlated cyclic high populations with invasions by Asiatic Pallas's grouse (*Syrhaptes paradoxus*) in Denmark. "Quail years" are listed by Saunders (1947) in England and by Westerskov (1947) in Scandinavia. The species has apparently decreased markedly in numbers in the last half century in Japan (Austin and Kuroda, 1953). In England it is just recovering after a long period of virtual extirpation (Moreau, personal communication).

Decimating agents.—Foxes, ermine, skunks, hamsters and hawks are listed as enemies of this quail by Dementev and Gladkov (1952); the crow (*Corvus brachyrhynchos*), Swainson's Hawk (*Buteo swainsoni*), snakes and harvest machines are mentioned by Jacobs (ms.). Owls expectedly take a heavy toll considering the nocturnal activity of the coturnix (Blanchet, 1939). Strung wires and other human agencies, especially for sport and market, are important decimating agents. Migration hazards seem to be of great importance. During migration lighthouses kill many quail (Meinertzhagen, 1924; Westerskov, 1947; Ticehurst, 1924). After a short spell of sea-fog, ships off the coast of Egypt sailed for an hour through floating masses of drowned quail (Moreau, 1928); Gurney (1901) found 8 to 10 Common Coturnix in the stomachs of sharks off the coast of France. In autumn practically the entire length of the north coast of Egypt is lined with nets and snares (Moreau, 1928). Post-harvest operations, i.e. the baling of windrows, may be more dangerous than the actual reaping of crops (Campbell, 1952).

Diseases and parasites.—The Common Coturnix is highly resistant to ulcerative enteritis (of uncertain infective agency) of Bobwhite (Kirkpatrick and Moses, ms.). Dr. F. R. Woodring (personal communication) found the Common Coturnix to be susceptible to erysipelas of turkey and swine in Nebraska. This disease is bacterial (*Erysipelothrix rhusiopathiae*) and communicable to man. The coccidium *Eimeria coturniceps* was found in the Common Coturnix in India (Chakravarty and Kar, 1946). The cestodes *Raillietina vivieni* in Indochina (Joyeux and Baer, 1935) and *Melroliasthes lucida* in England (Clapham, 1935) have been recorded. Likewise the following nematodes are listed as parasitizing coturnix: *Subulura coturnicis* (Yamaguti, 1941) in Japan and *Allodapa skrijabini* Semjonoff 1926, *A. noctuae gallinae* Semjonoff 1926, *A. suctoria* (Molin 1860), *Acuaria coturnicola* Semjonoff 1926, *Heterakis vesicularis* (Frohlich 1791), *Ascaridia compar* Schrank 1791 (or 1790?), *Harlertia obesa* Seurat 1915, *Cyrnea eurycerca* Seurat 1914 and *Agamospirura* sp. in the Don Region of U.S.S.R.; 39 per cent of 110 *C. coturnix* examined had these nematodes. Males were most frequently parasitized. The worms were most abundant in the small intestine but were also found in the caecum, under the corneus of the gizzard and in the bursa of Fabricius (Semjonoff, 1926). Cram

(1927) reported *Heterakis gallinae* Gmelin 1790. Ptushenko in the U.S.S.R. noted many tape worms in the young especially during drought (Demenkov and Gladkov, 1952). In Hawaii, Schwartz and Schwartz (1949) listed a hippoboscid fly, mites on head and primaries, lice and eye-worms.

Food

The Common Coturnix consumes a proportionately higher ratio of animal matter to vegetable matter than does the Bobwhite (Schwartz and Schwartz, ms.). These authors found that 21 stomachs in Hawaii contained 42 per cent animal matter and 58 per cent seeds by volume. The animal matter consisted mostly of insects and snails of the grass or ground-dwelling species, not of the flying or quickly moving insects. Kerc *et al.* (n.d.) lists 28 species of Coleoptera and 17 other forms of insects and 7 species of gastropods. Schwartz and Schwartz (1949) list 27 economically injurious animal forms from stomachs of Common Coturnix in Hawaii. Dementev and Gladkov (1952) list "snout beetles," Formicidae, Tineidae, Muscidae and other Arthropoda. In years of locust abundance this bird eats locusts in great quantities — but also the preying mantes. In Morocco, Meinertzhagen (1940) found this quail eating the small water snail, *Cochlicella acuta obesa* in fall. Witherby *et al.* (1941) note especially the larvae of *Agrotis*.

Seeds, mostly fallen seeds, (Stillwell and Smith, 1880; Dementev and Gladkov, 1952) are the chief vegetable matter eaten. Rice, wheat (Jones, n.d.), sesame (Bucknill, 1910), plantain and chickweed (Saunders, 1927), *Lolium*, *Brassica*, *Polygonum*, *Chenopodium*, *Rumex*, *Spergula*, *Stellaria*, *Plantago*, *Papayer*, *Vicia* (Witherby *et al.*, 1941) and *Ballota* (Dementev and Gladkov, 1952) seeds predominate. Kerc *et al.* (n.d.) list seeds of more than 130 forms from 28 families of plants in Hungary; Schwartz and Schwartz (1949) list seeds of more than 46 kinds for Hawaii. Berries of *Daphne gnidum* are a staple on the Canary Islands (Cullen *et al.*, 1952). Common Coturnix are not made sick by feeding upon *Arthusa cynapium* (poison hemlock) but may thereby become poisonous to a person who eats the flesh of the birds (Heim, 1928); this fact was experimentally confirmed by Sergeant (1941). Green matter is only rarely taken in the wild (Jones, n.d.; Kerc *et al.*, n.d.; Meinertzhagen, 1940) but is readily taken in captivity in the absence of water (Schwartz and Schwartz, 1949). Dementev and Gladkov (1952) mention sprouting plants as food. Their water requirements are apparently fulfilled by the insect diet (Schwartz and Schwartz, 1949) and by dew (Jones, n.d.) but they drink great quantities of water in captivity. In dry climes (Bourne, 1955) and in drought (Dementev and Gladkov, 1952) they drink from rivers and oases.

Grit is taken into their crops and stomachs (Schwartz and Schwartz, 1949; Dementev and Gladkov, 1952; Jones, n.d.).

HABITS

C. coturnix is most active at night and twilight (Dementev and Gladkov, 1952; and many other authors) and it is more susceptible to heat prostration than is the Bobwhite (Jacobs, ms.). Most of its food is taken in late afternoon; most birds collected in the morning or early afternoon had empty crops (Schwartz and Schwartz, 1949). Jones (n. d.) and others report dust bathing at noon.

Socially, the male is pugnacious toward competitors and toward its mate, while the female is less aggressive. Before egg laying in June, when flushed, the pair keep in close proximity (Ingram, 1908). While not otherwise gregarious, family bevy of both sexes unite to dust bathe but there is no permanent bevy formation (Schwartz and Schwartz, 1949). Migrating flocks, which may be large (Taka-Tsukasa, 1935), separate by day (Meinertzhagen, 1954). The male is so persistent at copulating in captivity that the female is unable to incubate; therefore, it is thought by game-breeders that the female must hide from him in the wild. Undoubtedly under natural conditions there is less aggression. Wild Common Coturnix often frequent poultry yards with domestic chickens in the Old World. They are difficult to flush except by dogs (Coward, 1926). They seldom rise twice (Meinertzhagen, 1954) and are often stepped upon. Sometimes when flushed by one sportsman, the birds fly blindly toward another (Gurney, 1901). The flight is swift, with rapid wing beats, direct, very low (6-15 ft.) and of flat and short trajectory (about 50 yards), ending with an indifferent glide; the bird usually remains where it alights (Schwartz and Schwartz, 1949). Even when several birds are found together they generally rise singly or in pairs (Jones, n.d.). Occasionally while in the air their flight changes to a "beautiful hovering motion" (Jones, n.d.). On the ground the bird runs swiftly to hide from danger (Dementev and Gladkov, 1952) — this may be in contradiction to Schwartz and Schwartz, above. It runs quickly and lightly but ungracefully with its very small tail hanging down and its neck drawn in, each step being accompanied by a slight nod of the head (Jones, n.d.). The English verb "to quail" takes its meaning from the habit of this bird of cowering from danger. It does not perch and at night (or day, as the case may be) roosts separately, even during very cold weather (Stanford, 1957).

ADAPTABILITY

It is ironic that this, the first bird species domesticated by man (The Mastaba of Mereruka, pt. 2, University of Chicago Art Institute, Sakkarah Expedition, 1938) should only in the 20th century be recognized for its potentialities as a pilot species for biological laboratory research. The adaptability of the bird to battery breeding cages, its prolificacy, and its accelerated ontogeny make it analogous to the white rat or fruit fly in its utility for laboratory experiments.

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Grit as an Ecological Factor¹

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ABSTRACT: The pheasant, a highly granivorous species, succeeds best in areas of high calcium concentration. Grains are normally low in calcium content, hence lime-containing grits act as a necessary source of this element. Gravel of the proper chemical composition is particularly significant in the diet of growing birds, and probably for hens during the laying season.

Recently glaciated regions where the till possesses high calcium characteristics represent the most suitable pheasant ranges. An example of this is the Minnesota, Dakota and northern Iowa area.

The indications are that grit possessing large amounts of magnesium, even though adequate in calcium, is undesirable and may even be deleterious.

The first to suggest a possible ecological role for grit was Leopold (1931). In discussing the peculiar distribution of pheasants and Hungarian partridge in the upper midwest, he hypothesized that various dietary factors, which included grit, might be responsible.

Data herein reported cover studies relating to the importance of grit in the welfare and distribution of the ringneck pheasant (*Phasianus colchicus*). Three aspects of the problem are recognized: 1) evidence for any nutritional relationship specific enough to be ecologically significant; 2) problems relative to measuring grit adequacy; and 3) evidence, positive or negative, that grit is important in pheasant ecology under natural conditions.

For gallinaceous birds, gravel (as a grinding agent) is generally recognized as an aid to the gizzard. However, any material hard enough to act as an abrasive seems to suffice; therefore, in this role the need for grit seems hardly singular enough to have ecological importance.

McCann (1939) has demonstrated that grit is also a source of required nutrient for the pheasant and must be classified under the category of a critical food. By using young, growing pheasants and feeding measured quantities of insoluble gravel (quartz) it was demonstrated that grit consumption quickly rose to extravagant levels with a manifest, frenzied craving for grit, which prevailed over their appetite for normal organic food. This reflected a nutritional need, since feeding with a supplement of bone meal (primarily tri-calcium phosphate) resulted in an almost immediate return to normal grit consumption. In another similar experiment, gravel consisting of glacial

¹ Funds for this study were supplied by the National Science Foundation. Facilities were graciously provided by the College of St. Thomas, St. Paul, Minn., and consulting advice was given by the Department of Chemistry, College of St. Thomas. Population data was made available by the Bureau of Game Research, Minnesota Division of Game and Fish.

till (low in phosphorous) had the same satisfying effect; and in still another experiment, powdered calcium carbonate produced a similar decline in grit consumption. These experiments indicated, therefore, that for the growing pheasant, grit is essential as a dietary source of the mineral element calcium.

According to the experiments of Dale (1955) with pheasants, calcium can also be critically important in the physiology of reproduction. And in this regard, recent studies reported by Hammond (1954) reveal that poultry, close relatives to the pheasant, store only enough calcium for six eggs, and that calcium is stored for no longer than ten days prior to egg laying.

Further evidence of the specific nutritional qualifications of gravel was indicated in an experiment by McCann (1938; 1939) in which experimental pheasants refused to utilize dolomitic limestone as a source of grit. This was interpreted as a deliberate abstention, since in every other study the birds consumed at least small daily quantities of grit.

More clearly suggestive of the inadequacy of grit with high magnesium content is the evidence with poultry. Alder (1927) found that pullets, after being fed dolomite grit for four months, became "... extremely nervous, very sensitive, and easily frightened. Production decreased, and the shell of the eggs became progressively thinner. Practically every bird in the pen developed diarrhoea or became very loose, as indicated by the droppings and badly soiled condition of the feathers of the abdomen. All of these conditions cleared up in a short time after substituting a practically pure carbonate limestone. . . ." He concludes that since magnesium forms a part of most deposits

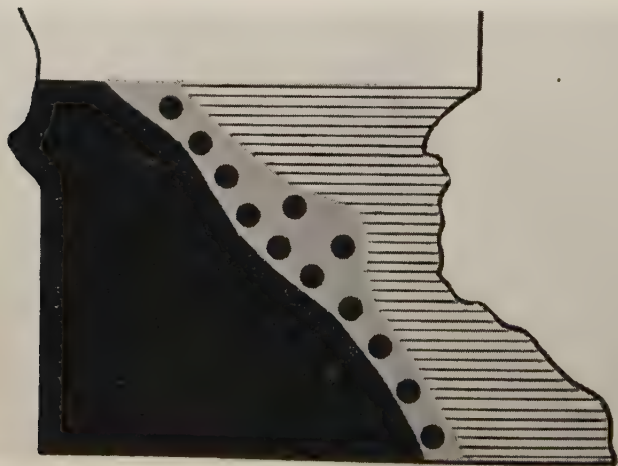


Fig. 1.—Relative abundance of pheasants in the state of Minnesota. (Solid: excellent to good; dotted: good to fair. Horizontal lines: fair to poor.)

resulted in growing chicks from adding 0.5 per cent magnesium to their diet, offered as carbonate. Buckner, Martin, and Inkso (1932) of limestone, limestone should not be used unless found free of magnesium. Mussehl, et al. (1930) found that a tendency toward rickets found that the addition of magnesium carbonate to the diets of chicks disturbed the calcium and phosphorous balance necessary for the normal formation of bones during the first six weeks' growth.

Significant to determining the chemical adequacy of grit is the fact that minerals are absorbed from food under the action of hydrochloric acid having a pH of 2.0 (Farner, 1942; Jull, 1951). Accordingly, the following technique of grit analysis was developed: to 15 grams of gravel is added 200 ml of .010N hydrochloric acid. This is then placed on a mechanical shaker for 15 minutes to simulate the action of the gizzard. Following this, a 50 ml aliquot is titrated, using the Versene method of calcium analysis with calcein as the indicator. The results are expressed as milligrams of CaCl_2 per 50 ml.

This technique proves particularly effective for low calcium samples, but it does not assay fully the calcium availability of high calcium samples, since 200 ml of acid is neutralized in less than 15 minutes under the influence of large quantities of calcium carbonate. Nevertheless, for practical purposes, the method reveals significant differences in calcium availability.

In the state of Minnesota, pheasants are most abundant in a triangular area covering the western and southern portions of the state (Fig. 1). To the east of this region, pheasant numbers gradually decline.

Pheasant population data was obtained from the Minnesota Division of Fish and Game. The information represents the accrued data from annual roadside censuses conducted since the 1940's. Numbers are expressed as birds per mile, on a county basis. Concurrently, sifted grit samples were collected from preselected collection sites. The collected samples were then analyzed chemically, using the method described.

The results, including population figures and grit analysis, are superimposed on the map of Minnesota in Figure 2. The data appear in the form of fractions, the upper figure representing the grit analysis results; the lower figures representing the population level for the county in question.

In the area of high pheasant abundance, to the west of the thin, oblique line (Fig. 2), the grit samples test homogeneously high in calcium content. In contrast, to the east both pheasant numbers and grit calcium figures are conspicuously low. For reasons previously described, the available calcium in the high-testing samples is no doubt even more surpassing.

The glacial till in the two areas is known to have had different origins. The western and southern areas of the state were glaciated by ice from the Keewatin Ice Center west of Hudson Bay, and the eastern areas of the state were covered by ice from the Labrador Ice

Center in northeastern Canada. Along the points where the two types of till meet, there appears to be considerable intermixing.

The southeastern corner of the state is unusual in never having been glaciated. The soil here consists of fine, wind-deposited loess, layed down during interglacial times. Grit in this soil is physically lacking. Outcroppings of ancient limestone occur in this area, but according to Prokopovitch and Schwartz (1956) much of this is dolomitic, in which the magnesium content is as high as 42 per cent. Crushed rock of this same material, in the absence of conglomerate gravel, is used as a road surfacing. Pheasant numbers in the counties of this area are notably low, averaging only 0.68 birds per mile for the entire area.

Two random grit samples were collected from western Wisconsin, which according to Dale (1955) is conspicuous for its low pheasant population. A random sample from St. Croix County contained 1.43 mgs of calcium; a similar sample from Pierce County tested 0.39 mgs. In contrast, two random grit samples from South Dakota, a state which is outstanding for its normally high pheasant numbers, tested as follows: a random sample from Codington County, 16.38 mgs; a random sample from Miner County, 18.59 mgs.

From the foregoing evidence it is the contention of the writer that grit of the proper chemical makeup (i.e., high calcium; low magnesium) is an ecological factor of paramount importance for the pheasant. In many situations it transcends in significance the factors of climate, cover, or any particular organic food. This is in harmony with the statement of Dale (1955) that the pheasant in North Amer-

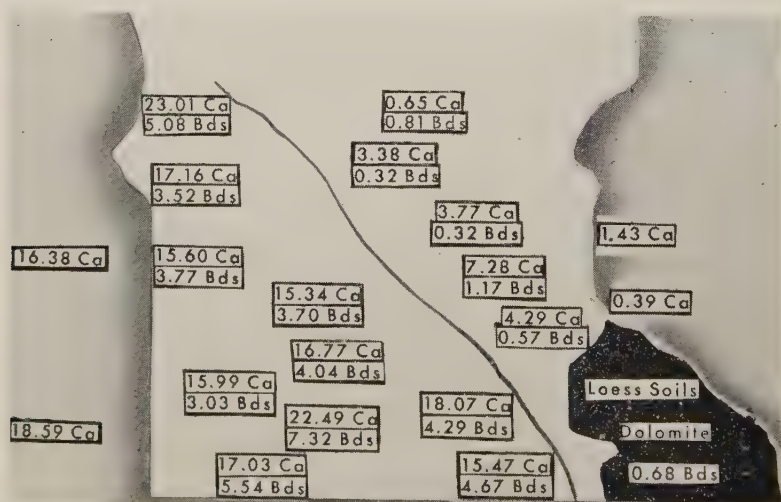


Fig. 2.—Grit-contained calcium, expressed in milligrams, compared with pheasant numbers, expressed as birds per mile. Figures from Wisconsin and South Dakota show only the calcium levels.

ica seems to have had its greatest success in areas with calcareous soils. It is the chemical nature of the grit, however, that evidence indicates is determinant.

DISCUSSION

The reason calcium-containing grit is so vital in the diet of pheasants probably arises from the fact that cereal grains play such an important part in their diet. Grains are known to be deficient in the mineral element calcium. This being the case, one might anticipate that the Hungarian partridge (*Perdix perdix*) would be as acutely influenced by the chemical nature of grit as is the pheasant, since the two species are about equally granivorous.

One might also speculate that among many other species of birds the need for calcium-containing grit is much less stringent and therefore less important ecologically. The grouse (*Bonasa umbellus*) has a diet comprising large quantities of herbaceous material and is equipped with large colic caeca which aid in extracting nutrient of low concentration. Its diet and digestive anatomy are somewhat comparable to those of a rabbit, and thus the grouse probably has no vital need for calcareous grit.

The raptorial species, which utilize the entire bodies of small vertebrates, more than likely have all their calcium requirements supplied by the endoskeletons of their natural prey.

Species whose diets are made up of large amounts of certain invertebrate animals may also be supplied with adequate amounts of mineral in their organic diet. Earthworms with their calciferous glands and terrestrial mollusks with their calcareous shells might be rich sources, to cite two examples.

Work by Grimshaw, *et al.* (1958) which shows a high level of calcium in caterpillar frass suggests the ability of insect larvae to concentrate this element, and thus to serve as a possible dietary source of calcium.

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Observations on the Life Histories of Turtles (Genus *Pseudemys* and *Graptemys*) in Lake Texoma, Oklahoma

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ABSTRACT: Aspects of the life histories of *Pseudemys scripta elegans* and *Graptemys pseudogeographica ouachitensis* (Reptilia: Testudines) were studied in Lake Texoma, Oklahoma. Variation in the color patterns of the two species is considered. Males of *Pseudemys* are sexually mature at a plastron length of 9.0 to 10.0 cm; females at 17.4 to 19.3. The realized annual reproductive capacity of a female *Pseudemys* is estimated to be 26.4 eggs (3 clutches; 8.8 eggs per clutch). Some males become sexually mature in their third year; females in their fourth. Males of *Graptemys* are sexually mature at a plastron length of 7.0 cm; females at 15.0 cm. Each *Graptemys* female lays approximately 19.5 eggs per year (3 clutches; 6.5 eggs per clutch).

The elongation of the tail and third claw of the forelimb are secondary sexual characters in males of both species. Growth in both species progresses rapidly prior to maturity, however, *Graptemys* females seemingly grow more slowly than *Pseudemys* during this period. Rapid fluctuation of the water level may result in a slowing of growth in *Pseudemys*, but the evidence is only suggestive, not conclusive. Alternation of habitats along the shoreline due to the changing water level is believed to be responsible for the nomadic behavior of *Pseudemys* as well as in determining the quality and quantity of food available.

The abundance of the red-eared turtle, *Pseudemys scripta elegans* Wied, and the Ouachita map turtle, *Graptemys pseudogeographica ouachitensis* Cagle, in Lake Texoma, made possible a comparative life history study at the University of Oklahoma Biological Station, Marshall County, 2 miles east of Willis.

Acknowledgments.—I am grateful to Dr. Carl D. Riggs, Director of the Biological Station for permission to utilize facilities in his care. I am indebted further to Dr. Harley P. Brown of the University of Oklahoma Department of Zoology for the analysis of the animal material in the contents of digestive tracts of selected turtles, and to Dr. George J. Goodman of the University of Oklahoma Department of Botany for selected botanical determinations. Finally, thanks are extended to Drs. Fred R. Cagle and Henry S. Fitch for constructive criticism of the manuscript.

METHODS

Most data were obtained from turtles trapped in hoop nets in June and July, 1954. All individuals were either marked and released or examined by dissection. Measurements were made with a millimeter rule, a Vernier caliper or with the instrument described by Cagle (1946:687). Unspecified measurements in the text refer to plastral length. Selected specimens were dissected to determine sex,

attainment of sexual maturity, reproductive potential and food habits. Ovaries and oviducal eggs as well as stomach and intestinal contents of selected specimens were removed and preserved; also, permanent slides of selected sperm smears (Wright's stain) were prepared.

In the summer of 1953, Dr. Bryan P. Glass marked turtles of several species, recording the sex and length of carapace; all were released at the shoreline just south of the Biological Station. A few of these, recovered in the summer of 1954, provided data on movement and growth. Many others were marked and released at the point of capture; data recorded included locality, sex, and plastral length. The system of marking consisted of boring a hole in a marginal plate and fastening a numbered metal tag.

Several turtles utilized in this study were collected by hand, seined, or trapped in gill nets. Most turtles were trapped in three collapsible 3-hoop nets of heavy cord or two non-collapsible metal fyke nets; the mesh-size prevented the escape of all turtles exceeding 4.0 cm. The traps, used simultaneously, were baited with freshly-chopped fish and occasionally with other meat scraps. The number of traps and trapping success varied with location. Traps were moved from time to time. This trapping procedure revealed that *Pseudemys scripta* was the most abundant species. Of 156 turtles trapped from June 14 to July 12, 1954, 100 (64%) were *Pseudemys scripta*, 24 (15%) were *Graptemys pseudogeographica*, 19 (12%) were *Trionyx spinifer*, 8 (5%) were *Chelydra serpentina*, 3 (2%) were *Kinosternon subrubrum*, 1 (1%) was *Pseudemys floridana*, and 1 (1%) was *Trionyx muticus*.

The largest number of turtles trapped in a single net at any one time was 12 *Pseudemys scripta*. The nets caught specimens of *Pseudemys scripta* and *Graptemys* of all sizes and both sexes; only one adult female *Graptemys* was obtained.

Turtles of the genus *Graptemys* are considered to be partial to the deeper waters of rivers having a moderate current about emergent fallen trees, brush piles and other debris. Such habitats, which were explored during the writer's participation in Tulane University field expeditions in the summers of 1952, 1953, and 1954, yielded many specimens. Within the known geographic range of the genus, I visited a lentic habitat (Lake Concordia, Concordia Parish, Louisiana) only once. This ox-bow lake of the Mississippi River has extensive beds of submerged vegetation. Three specimens of *Graptemys kohni* were collected by hand at night in approximately four and one-half hours, employing the technique described by Chaney and Smith (1950); other individuals were seen but not collected. To my knowledge there are no published records of *Graptemys* having been collected in lentic habitats. The exploration of large ponds, lakes and impoundments undoubtedly will reveal at least some species of *Graptemys* to be more common in these situations than is currently believed.



Fig. 1.—Upper, mouth of Buncombe Creek from west bank near the Biological Station; note the barren aspect of the lake shore. Photograph taken on February 24, 1951, in a period of low water. Fig. 2.—Lower, inundated area about one mile west of the Biological Station. Photograph taken on June 19, 1951.

DESCRIPTION OF AREA

Lake Texoma was impounded in 1944 for flood control and hydro-electric power by the Denison Dam across the Red River between Grayson County, Texas, and Bryan County, Oklahoma. The conservation level or normal power pool elevation of 617 feet above mean sea level covers 93,085 acres, and the drainage basin of Lake Texoma occupies 38,291 square miles. The lake has a shoreline of approximately 650 miles and a dendritic shape; it is divided into the Red River arm separating Texas and Oklahoma, and the Washita arm that forms the boundary between Marshall and Bryan counties, Oklahoma.

The Biological Station is at the mouth of Buncombe Creek on its west bank. The surrounding area is essentially a transitional zone between the eastern blackjack-post oak forest and the western mixed grass prairie, the Osage Savannah District of Blair and Hubbell (1938:433). The marked fluctuation in water level (Figs. 1 and 2) prevents the establishment of permanent stands of aquatic vegetation in the lake; small patches of pondweed (*Potamogeton* sp.) and smartweed (*Polygonum* sp.) occur occasionally. The fluctuation of water level in the years 1949 through 1953 is presented to give some idea of the degree and rapidity of fluctuation (Fig. 3). After torrential rains, water rapidly inundates the adjacent, relatively level, areas, and often strands reptiles, and occasionally small mammals, in the boughs of willow trees. The salt cedar, *Tamarix gallica*, is often abundant when the receding water level exposes the shoreline long

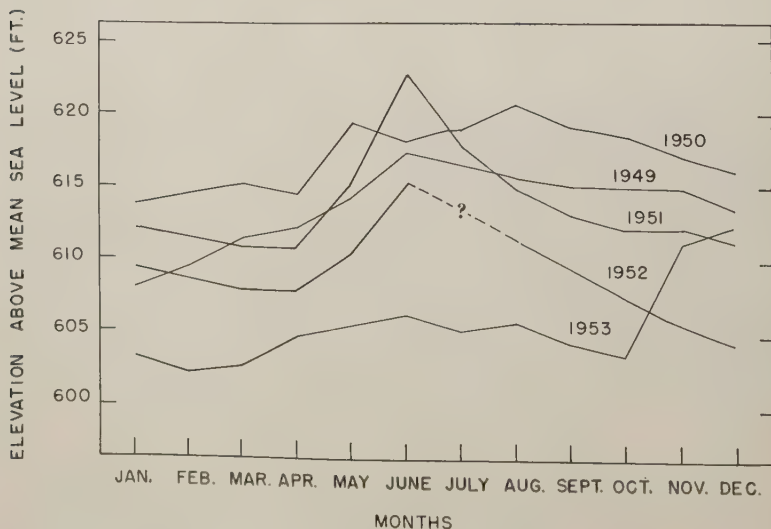


Fig. 3.—The fluctuation of water level in Lake Texoma in the years 1949 through 1953. Monthly values represent the average water levels.

enough to permit its establishment. The fogwort, *Lippia incisa*, and Bermuda grass, *Cynodon dactylon*, often dominate an extensive low cover along the shoreline; thickets of black willow, *Salix nigra*, often encroach on the lake shore. Wave action on Lake Texoma is common and often severe. The lake bottom is chiefly sand and clay, and the water is usually turbid. Basking sites for turtles, fallen trees and debris, are at a premium; tree stumps are often exposed and utilized. Sublette (1955) has commented on the physico-chemical and biological features of Lake Texoma, and Riggs and Bonn (1959) have discussed the general environmental factors and fishes. Carpenter (1955) has mentioned species of amphibians and reptiles occurring in the Lake Texoma area.

Pseudemys scripta elegans Wied

Red-eared Turtle

Of 127 individuals utilized in this study, 35 were preserved. All are in the collection of the University of Oklahoma Museum, Division of Zoology and bear the following catalogue numbers: 27131-37, 27158, 27299-300, 27307, 27311-16, 27339-42, 27388, 27555-61, 27570-72, 27577-79, 27582-83, 27595. In other parts of its range this subspecies has been the subject of intensive research by Cagle (1950).

Description.—The configuration of the red postocular blotch and the minimal size of completely melanistic males are subject to geographic variation.

Specimens having an isolated, oval, black-bordered, red blotch back of the eye, and elongated plastral blotches, which have been assumed to be indicative of intergradation with *P. s. gaigeae*, have been reported from northwestern Louisiana and central Texas (Cagle, *op. cit.*:34). The variation in configuration of the postocular blotch in specimens from southwestern Oklahoma has been mentioned by Webb and Ortenburger (1953:88). Of 120 individuals from Lake Texoma, 59 (49%) exhibit only a slight narrowing of the enlarged, red postocular blotch and have a broad bar entering the eye on both sides of the head (No. 27558). Thirty-one specimens (26%) have the smaller anterior portion of the postorbital bar clearly separated from the larger posterior section on both sides of the head (No. 27583); some of these have a dark vertical line separating the two blotches (No. 27582). Only 5 per cent of the population from northwestern Louisiana had two separate postocular red marks. The remaining 30 individuals (25%) have intermediate patterns, some possessing a narrowed anterior segment (No. 27578), others having the anterior portion constricted to the point of separation (No. 27342), and many have a combination of patterns on either side of the head (Nos. 27577, 27557). The separation of the postocular blotch from the orbit seems to be due to individual variation and not to intergradation with *P. s. gaigeae*.

Males of *Pseudemys s. elegans* become dark with an obliteration of the pattern on the soft body parts, carapace and plastron (Viosca,

1933). The assumption of melanism is not coincident with the attainment of sexual maturity. This melanism first becomes apparent on the plastron, then on the carapace and finally on the soft parts of the body. Completely melanistic individuals may have a plastron as short as 15 cm and all individuals in which it exceeds 17 cm are completely melanistic. Two of nine males in the 15.1 to 16.0 cm size-group, and one of four in the 16.1 to 17.0 cm size-group were completely melanis-

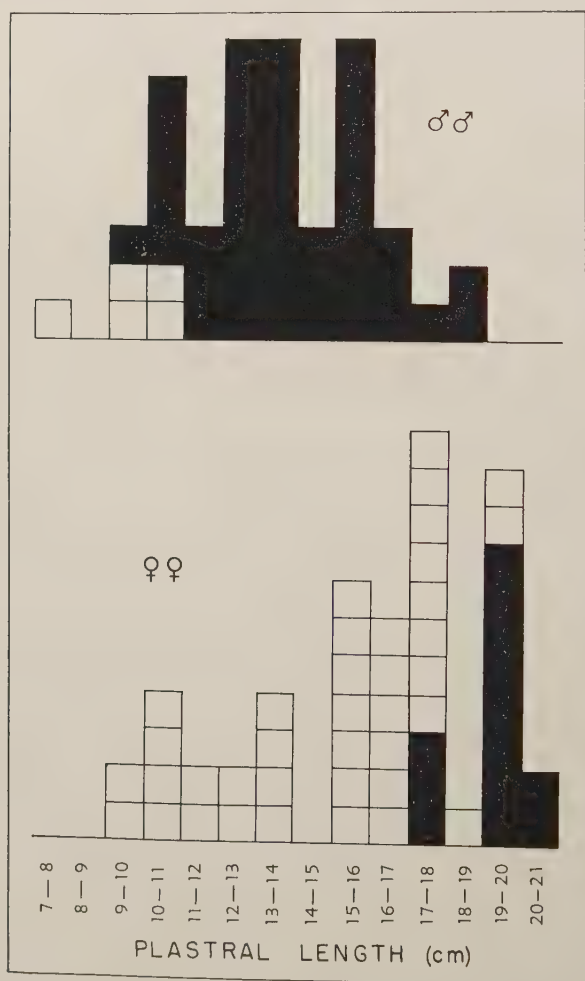


Fig. 4.—Size distribution of 98 *Pseudemys s. elegans* collected from June 17 through July 12, 1954. Open squares indicate immature individuals; solid squares indicate sexually mature individuals. Each square represents one specimen.

tic. The smallest completely melanistic male from Lake Texoma (15.2 cm) is larger than the smallest reported from eastern Texas (10 cm) or Tennessee and Illinois (13 cm) (Cagle, *loc. cit.*). Large adult females occasionally have plastrons that are as much as 80 per cent darkened.

Size at sexual maturity.—Cagle (1948:108) concludes that males become sexually mature when they reach a plastral length of 9 to 10 cm. Of 47 males, ranging in plastral length from 7.7 to 18.4 cm, 42 (89%) were sexually mature (Fig. 4). All male turtles exceeding 11.0 cm were assumed to be sexually mature on the basis of well-developed secondary sexual characters (enlarged tail and claws of forelimbs). The presence of sperm in the vasa deferentia or a portion of the testis was the criterion for sexual maturity in the remaining individuals, except two. Of the latter, one (10.7 cm) having well-developed secondary sexual characters was considered sexually mature, whereas the other (7.7 cm), was dissected and considered immature on the basis of small, undeveloped testes and vasa deferentia. The male of this species in Lake Texoma becomes sexually mature when its plastron has attained a length of 9 to 10 cm.

Some adult males differ from females of the same size in having a carapace with straight or parallel sides, that is to say, there is no curvature in the region of the bridge; this condition is accentuated by a posterior flaring of the carapace.

Cagle (1950:44) has shown that some females are sexually mature when the plastron is 15.0 cm in length; there was no apparent difference between populations from Illinois, Tennessee, and Louisiana. Of 51 female turtles ranging from 9.4 to 20.3 cm, 13 (24%) were considered sexually mature (Fig. 4). Of 22 specimens that were dissected, eight were considered sexually mature because they had oviducal eggs or corpora lutea or ovarian follicles exceeding 15 mm in diameter; these eight females included two of seven in the 17.1 to 18.0 cm size-group, four of six in the 19.1 to 20.0 size-group, and two of two in the 20.1 to 21.0 cm size-group. Five additional females, 17.5, 19.2, 19.7, 19.9 and 19.9 cm, were not dissected but were considered sexually mature on the basis of a decided cessation of growth as revealed by an examination of the growth rings. All remaining females (not dissected) showed no retardation of growth and were considered immature.

Data from four additional dissected specimens from Lake Texoma (not included in Fig. 4) are as follows: No. 27131, secured on May 19, 1951, 18.5 cm, sexually mature; No. 27299, secured on July 8, 1951, 18.0 cm, immature; No. 27300, secured on July 8, 1951, 19.3 cm, sexually mature, and a specimen taken on July 21, 1954, 18.1 cm, sexually mature.

My data indicate that some females are sexually mature when the plastron is 17.4 cm in length. Although the size of the smallest sexually mature female is unknown, the data suggest a larger size than that reported by Cagle.

Eggs.—Fifty-three oviducal eggs were 18.9 to 23.6 (mean 21.4) mm wide, and 32.6 to 39.4 (mean 37.6) mm long. The mean measurements of these eggs do not differ appreciably from corresponding measurements of oviducal eggs of populations from Illinois and Louisiana (Cagle, *op. cit.*:38). The six females containing oviducal eggs were 18.0, 19.1, 19.4, 19.9, 20.3, and 20.3 (mean 19.5) cm; the number of eggs varied from one to 12 (mean 8.8). There is no indication of a correlation of the size or number of eggs with plastral length. Counts of oviducal eggs may be biased, as in some individuals one or more eggs may have been deposited previously, or, if an extended breeding season is demonstrated and if more than one clutch per season are deposited, counts of oviducal eggs may include eggs of the previous clutch that were not deposited.

Reproductive potential.—The length of the annual breeding season for females in Lake Texoma is unknown. Whatever length it is, the breeding season is long enough for some of them to deposit three clutches as shown by individual females that contained oviducal eggs, ovarian follicles exceeding 15 mm in diameter, and corpora lutea of different sizes that exceed in number the number of oviducal eggs.

Ovarian follicles larger than 15 mm in diameter are considered to comprise, at least partly, the next clutch that will be deposited in the current season. Follicles of this size possibly are retained until the following year or some may undergo regression. Cagle (*loc. cit.*) reported follicles exceeding 10 mm in diameter in females examined in September and October from Louisiana and Illinois.

The different sizes of the corpora lutea that exceed in number the number of oviducal eggs suggest that a clutch had previously been deposited in the same season (year). The maximum diameter of the largest corpora lutea, which represent ovulation points of eggs contained in the oviducts, is 8 to 9 mm. The maximum diameter of the largest corpora lutea in turtles that contained no oviducal eggs, collected in the breeding season, is 5 to 6 mm. The length of time that the eggs remain in the oviduct, and the length of time between their deposition and ovulation of the succeeding clutch is unknown. The corpora lutea presumably decrease at least 3 to 4 mm in diameter between ovulation and deposition and perhaps more between successive ovulations. Assuming an equal and continuous rate of regression of all corpora lutea, those representing ovulation points of the last clutch of the breeding season probably regress to corpora albicantia by the beginning of the next annual breeding season. Risley (1933:694) states that the eggs of *Sternotherus odoratus* remain in the oviducts for a period of from 20 to 35 days. If the eggs of *Pseudemys s. elegans* remain in the oviduct for this length of time, corpora lutea probably regress completely (about three mm every 27 days) in approximately three months. Edgren (1960:61), however, writes that the life of the egg in the oviduct of *S. odoratus* must be between five and eight weeks.

Follicles of the most enlarged groups in the ovaries of each of the 11 sexually mature females varied in extremes from 10 to 21 mm in

diameter. Counts of these follicles indicated an average reproductive potential of 16.2 eggs per clutch, which is almost twice the 8.8 revealed by counts of oviducal eggs. This discrepancy is due to the inadvertent inclusion of developing follicles that are not representative of the succeeding egg complement; also, some may remain unfertilized and others may become atretic. Follicles considered atretic are red-brown; the color is darker in the smaller follicles. The largest follicle considered to be undergoing atresia was 12 mm in diameter and a pale red-brown, contrasting with the yellow-orange of the viable follicles.

All 11 females, collected from May 19 to July 21, contained ovarian follicles 15 mm in diameter or larger. Five of seven specimens collected in June contained oviducal eggs, whereas one of three collected in July contained one egg in the oviduct. The presence of one oviducal egg on July 12 in a female having no corpora lutea indicates retention of this egg for a considerable length of time (equal to that necessary for complete regression of the corpora lutea), and presumably the egg was a remnant of a previous deposition. The two females collected on July 8 and May 19, which had no oviducal eggs or corpora lutea to indicate recent deposition, but possessed follicles 14 to 17 mm in diameter, suggest the approach of the first ovulation for the current breeding season; these females may or may not be in their first reproductive season. The collection date of July 8 suggests that the first clutch of a season need not be deposited at the beginning of the breeding season, and that a female may deposit only one clutch per season, whereas other females may deposit two or three.

Lake Texoma females are apparently capable of depositing three clutches per season. The deposition of repeated clutches in a long egg-laying season has been mentioned for *Chrysemys* (Cagle, 1954:229) and other turtle species (Cagle, 1950:38). The total annual reproductive capacity of some females may amount to 36 eggs (maximum of 12 per clutch; maximum of 3 clutches per season), but the realized annual reproductive capacity is estimated to be approximately 26.4 eggs (mean of 8.8 per clutch; maximum of 3 clutches per season).

Growth.—The estimate of growth is based on calculated increments from measurements of growth rings, which has been shown to be valid for *Pseudemys s. elegans* (Cagle, 1946).

The calculated plastral length of 26 individuals at hatching was 2.3 to 3.9 (mean 3.1) cm; of these eight were males, 2.6 to 3.8 (mean 3.1) cm, and 18 were females, 2.3 to 3.9 (mean 3.1) cm. At the end of the first year of growth (the first growing season) seven males were 4.1 to 6.3 (mean 5.4) cm, and had increased 1.5 to 3.2 (mean 2.2) cm; 18 females were 4.2 to 7.8 (mean 6.2) cm, and had increased 1.7 to 4.7 (mean 3.1) cm. At the end of the second year of growth, six males were 6.0 to 8.3 (mean 7.1) cm, and had increased 1.2 to 2.7 (mean 1.9) cm; 12 females were 6.2 to 11.3 (mean 9.1) cm, and had increased 0.9 to 4.5 (mean 2.8) cm. At the end of the third year of growth, four males were 7.4 to 10.9 (mean 8.9) cm, and had increased

0.8 to 2.7 (mean 1.2) cm; seven females were 8.0 to 14.0 (mean 11.4) cm, and had increased 0.9 to 3.5 (mean 2.2) cm. The ring bordering the femoral plate at hatching in 26 turtles examined was still evident in three females that had rings representing the termination of growth

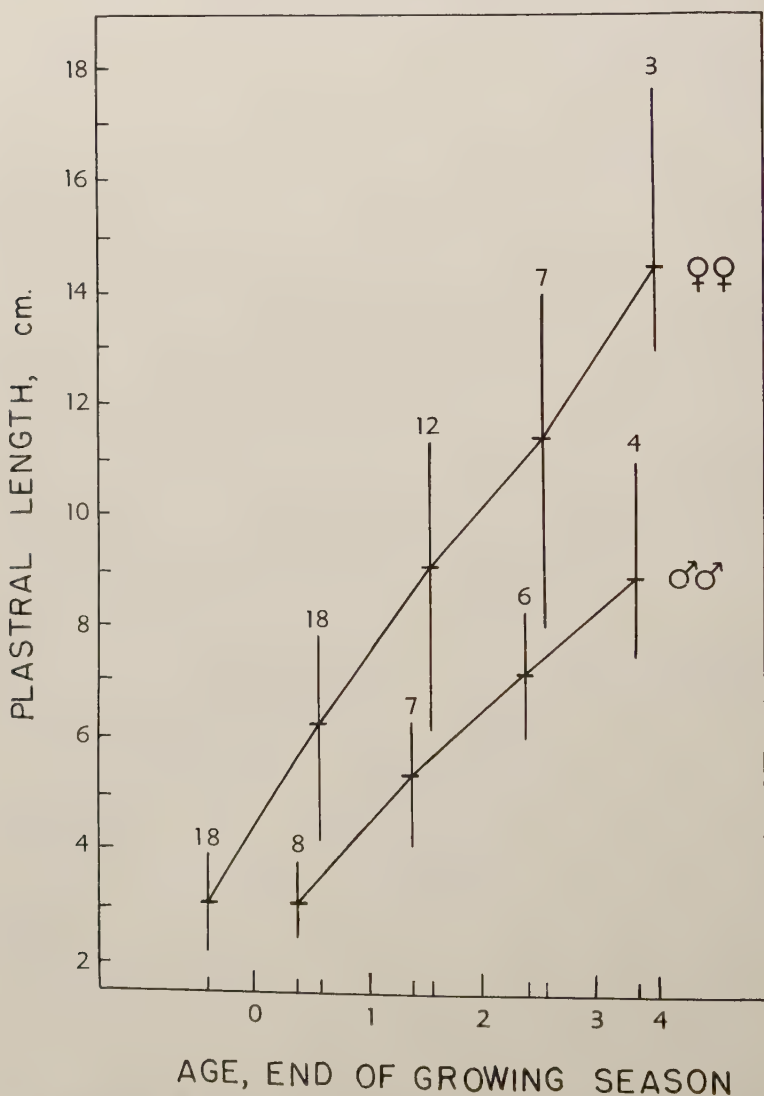


Fig. 5.—Early growth of *Pseudemys s. elegans*. Vertical lines indicate the range in length of plastron; the diagonal lines connect the means. The figure above each line represents the number of specimens.

in the fourth year; these indicated a size of 12.9 to 17.6 (mean 14.5) cm, and had increased 1.3 to 3.8 (mean 2.6) cm. A growth curve is plotted from the calculated plastral lengths for these individuals (Fig. 5). Thus, some males become mature in their third year (one, 10.9 cm, No. 27133), and females in their fourth (one, 17.6 cm, No. 27560). Growth is seemingly more rapid and variable in females. The variation in growth is attributed to individual variation, to the inclusion of individuals that are representative of clutches deposited at different times in the same breeding season, and to those whose seasonal increments of increase occurred in different growing seasons.

Segments of the growth curve were calculated for 38 males and 42 females in which the ring bordering the femoral plate at hatching was not evident and thus the age was unknown. These growth segments were assigned to arbitrary size-groups in each growing season and the average increments of increase within each size-group determined (Table I). Despite apparent exceptions owing to individual variation or lack of specimens, the general tendency is a slowing trend of growth with larger size in both sexes, the greatest retardation occurring at the size of attainment of sexual maturity. The largest increments of increase for any individuals were those of a male that increased 6.1 (4.1 to 10.2) cm in the growing season of 1952, and a female (No. 27131) that increased 5.2 (7.4 to 12.6) cm in the growing season of 1949.

Data on growth for five recaptured individuals are presented in Table II. All three males were sexually mature. Two females, both immature, showed relatively the largest increments of increase.

Analysis of growth as affected by varying ecological factors is difficult because of extreme variation with sex and size. However, variation in growth for the population here studied is probably correlated with the fluctuation in water level. In the growing season of 1953 six immature males increased an average of only 0.9 cm (Table I), whereas the average increment of increase for males in the same general size-group in other growing seasons exceeded 2.1 cm. Two immature females in the growing season of 1953 increased an average of 1.4 cm, whereas those in the same general size-groups in other growing seasons (except possibly 1952) exceeded an average of 2.6 cm. An examination of Figure 3 reveals that the lowest elevation of water level occurred most consistently in 1953. Possibly a lowering of the water level for a significant length of time decreases the availability of the food supply, which in turn, retards growth. However, the increments for the other size-groups of immature females in the growing season of 1953 are not noticeably retarded as one would expect; possibly only certain-sized individuals are affected. The arbitrary selection of size-groups, which overlap within each growing season and are not exactly comparable between growing seasons, obscures an evaluation of size-group comparisons. Although suggestive, these data do not clearly demonstrate that water fluctuation is a factor influencing growth rate.

Food.—Presumably a direct influence of fluctuation of water-level is on the food supply, but omnivorous habits (Cagle, 1950:48) allow

TABLE I.—Growth rates in *Pseudemys scripta elegans* of different size groups in different growing seasons

Year	Average extremes in plastron length of turtles at the beginning and end of growing season (cm)	Number of increments in sample	Average increment of increase in plastron length (cm)
Males (38)			
1949	7.5-10.3	1	2.8
1950	4.4-6.6	1	2.2
	7.7-9.2	1	1.5
	10.4-12.2	2	1.8
	16.5-16.9	1	0.4
1951	6.0-8.9	2	2.9
	9.0-11.1	5	2.1
	13.3-14.5	1	1.2
1952	6.4-9.2	5	2.8
	10.6-11.8	10	1.2
	12.3-13.0	2	0.7
	14.2-14.6	2	0.4
1953	8.7-9.6	6	0.9
	10.7-11.9	7	1.2
	11.8-12.7	5	0.9
	12.8-13.6	8	0.8
	14.5-15.2	8	0.7
Females (42)			
1949	4.0-7.3	1	3.3
	7.2-10.2	5	3.0
	12.1-15.6	1	3.5
	14.9-18.7	1	3.8
1950	5.5-8.2	5	2.7
	8.0-10.6	4	2.6
	10.2-13.3	3	3.1
	12.5-16.1	2	3.6
	15.6-18.0	1	2.4
	18.7-19.1	1	0.4
1951	5.2-7.8	1	2.6
	8.6-11.3	13	2.7
	12.3-13.6	2	1.3
	14.1-16.2	6	2.1
	17.2-18.1	3	0.9
1952	6.9-10.0	4	3.1
	11.6-13.0	16	1.4
	13.8-15.2	6	1.4
	17.0-18.2	8	1.2
1953	6.2-9.5	2	3.3
	10.5-11.9	2	1.4
	12.6-14.7	19	2.1
	15.6-17.2	9	1.6
	17.5-19.0	1	1.5
	18.8-19.3	6	0.5

this species to thrive in areas subject to an alternating availability of different food supplies. Individuals have been observed feeding on insects, fish and other vertebrate remains in captivity. In a period of inundation, the stomach and intestine of two females (15.1 and 15.6 cm) collected on June 21, 1954, and one female (20.3 cm) taken on July 12, 1954, were extended with large quantities of the herb, *Lippia incisa*. One specimen, showing no apparent ill effects when alive, had the barbed end of a small fish hook protruding from the stomach.

Movement.—Information concerning the extent of movement is based on the distance between points of release and capture for four recaptured turtles. One male, bearing metal tag number 4230, had moved a distance of approximately one and one-half miles from July 23, 1953, to July 21, 1954, whereas the female, No. 127, moved about one-third of a mile from sometime in July, 1953, to June 22, 1954. Another male, No. 4213, had moved approximately one mile from July 20, 1953, to June 21, 1954. The other male, No. 4241, which had moved about two-thirds of a mile from July 23, 1953 to June 18, 1954, was recaptured on June 20, 1954, and had moved about the same distance in this two-day period. Data obtained by Cagle (1944:18) for this subspecies in southern Illinois suggest that each turtle tends to remain within one area of a body of water. My data indicate much movement, but the marked turtles were not initially released at the site of original capture and may have made homing movements in some instances. However, the recaptured male, No. 4241, traveled approximately two-thirds of a mile in two days after being released at the site of capture.

A nomadic behavior is suggested and is perhaps stimulated by the change in habitat and morphometry due to the rapid fluctuation in water level; this change possibly prevents the recognition of any localized habitat, and the consequent establishment of a home range. Cagle (*op. cit.*:27) suggested that the transfer of individuals of *Chrysemys* to a strange habitat effects a nomadic behavior.

Graptemys pseudogeographica ouachitensis Cagle

Ouachita Map Turtle

Of 49 turtles utilized in this study, 37 were preserved and bear the following catalogue numbers: University of Oklahoma Museum, Divi-

TABLE II.—Growth of five recaptured *Pseudemys scripta elegans*

Number on metal tag	sex	carapace length (cm)				increment of increase (cm)
		release		recovery		
102	female	Jun. 18, '53	7.1	Jul. 16, '53	7.9	0.8
127	female	Jul. ?, '53	8.7	Jun. 22, '54	13.1	4.4
4213	male	Jul. 20, '53	13.4	Jun. 21, '54	15.1	1.6
4230	male	Jul. 23, '53	12.2	Jul. 21, '54	14.4	2.2
4241	male	Jul. 23, '53	12.9	Jun. 18, '54	13.8	0.9
		Jun. 18, '54	13.8	Dec. 18, '55	15.6	1.8

sion of Zoology (UOMZ) 26911-12, 27130, 27327, 27551-54, 27564-65, 27567-68, 27573-76, 27580-81, 27584-92; University of Kansas Museum of Natural History (KU) 40167-74, skeletons have since been prepared of these specimens; Tulane University (TU) 16661-1, 17300-1. This material affords hitherto unrecorded information concerning aspects of the species' natural history as well as descriptive comments to augment our knowledge of geographic variation.

Description. -Turtles of this subspecies from Lake Texoma differ in certain respects from the type description (Cagle, 1953:15), and their brief description here will serve to supplement that by Carr (1952:211) based on specimens from Medicine Creek, Comanche County, Oklahoma.

The measurements (in cm) of two hatchlings (TU 17300-1) in their first year of growth are, respectively, as follows: length of carapace 4.0, 4.7; width of carapace 3.7, 4.3; height of carapace 1.8, 2.0; length of plastron 3.6, 4.1; width of head 0.9, 0.9. There are 37 and 43 longitudinal light stripes on the neck, 10 and 11 on the anterior surface of the forelimb, and 11 and 13 on the upper surface of the hindlimb. The postocular blotch is oblong and smaller than (two-thirds to three-fourths) the height of the orbit; the blotch is not in contact with the upper longitudinal light stripes in TU 17300 but narrowly in contact anteriorly in TU 17300.1. Eight light longitudinal neck stripes (3 wide stripes flanked by 5 narrower stripes) enter the orbit. The lateral yellow spots on the ventral surface of the lower jaw may be nearly circular like the central spot or more elongate. The marbled plastral pattern, more concentrated than that figured by Cagle (*op. cit.*:15, fig. 3B), is more or less symmetrical and comprises an estimated three-fourths of the plastral area. The bridge and under-surface of the marginals are extensively dark-marked, and the black of the knobs on the first, third and fourth vertebrae is less extensive than that figured by Cagle (*op. cit.*:13, fig. 2A).

The head is not conspicuously broadened in nine adult females. The length of plastron (15.4 to 17.0, mean 16.2 cm) is 6.8 to 7.6 (mean 7.1) times the width of the head (2.2 to 2.4, mean 2.3 cm). The size of head cannot be compared with that reported by Cagle (*op. cit.*:14) because width of carapace was not recorded by me.

A feature of coloration (in life) of adult males and females is not mentioned by Cagle. The network of light lines on the carapace, the wide circular marks on the ventral surface of the marginals, and especially the dorsal and lateral neck stripes are orange (not yellow). Occasional individuals of *G. kohni*, and *G. p. ouachitensis* in other parts of its range, may possess the orange striping on head and neck, but it is not a consistent feature of the population. A kyphotic specimen from Marshall County has been mentioned by Carpenter (1958:116). The photographs of two adult females (Fig. 6) illustrate the habitus of specimens from Lake Texoma.

Some of the variation noted above has been mentioned by Cagle (*op. cit.*:15). Briefly, the population in Lake Texoma differs from

the type description in 1) the larger number of stripes on the neck, anterior surface of the forelimb, and upper surface of the hindlimb; 2) the usually isolated, oblong, postorbital blotch that is smaller than the height of the orbit; 3) the larger number of stripes that enter the orbit; 4) the extensive plastral pattern in hatchlings; 5) the reduction of black on the vertebral knobs in hatchlings, and 6) the orange striping.

Size distribution.—Of 24 females (all collected within a 24-day period in mid-summer) there is a decided prominence of immatures (Fig. 7). This contrast in size distribution of female *Graptemys* and *Pseudemys* (see Fig. 4) reflects the different food habits of the two species and the collecting method used. Large adult females of *Graptemys* are seldom seen, and then are extremely wary and difficult to catch. The majority of the adult female *Graptemys* used in this study were obtained from gill nets or seined from shallow areas.

Size at sexual maturity.—Cagle (*op. cit.*:12) lists the extremes in size of adult males as 7.8 and 9.2 cm; his criteria for sexual maturity are presumably the elongation of the nails of the forefeet (*op. cit.*:14) and the enlargement of the tail. Of 13 males from Lake Texoma with extremes of 4.4 and 8.7 cm, nine were sexually mature; the smallest mature one was 7.3 cm. Only six males were dissected and the testes smeared for the presence of sperm; five, which had pigmented vasa deferentia, were adult (7.5, 7.8, 8.3, 8.3, and 8.5 cm), and one was immature. Four other males (7.3, 7.7, 8.4 and 8.7 cm) were considered mature on the basis of well-developed secondary sex characters. This suggests a plastral length of approximately 7.0 cm as the size of attainment of sexual maturity. The marked change in the relation of length of tail to length of plastron in males at the size of attainment of sexual maturity has been clearly demonstrated for *Pseudemys s. elegans* (Cagle, 1948:108), *Chrysemys picta* (Cagle, 1954:232), and *Trionyx spinifer emoryi* (Webb, 1956:121), and is apparent in adult males of other species of turtles. Figure 8A reveals an increase in length of tail as male specimens of *Graptemys* reach a size of 7.0 cm. The cloacal opening extends beyond the posterior edge of the carapace in adult



Fig. 6.—Adult females of *Graptemys p. ouachitensis*; both have plastron lengths of 16.7 cm. Left, KU 40171; right, UOMZ 27581.

males; the distance measured was from the rear edge of the carapace to the anterior lip of the cloaca. Cagle (1948:108) has also shown the length of the claws of the forelimb to be a secondary sex character in *P. s. elegans* as well as in male *Chrysemys* (1954:232). Male specimens of *G. p. ouachitensis* also show a decided lengthening of the third claw of the forelimb (measured in a straight line from its base to tip) when a plastral length of 7.0 cm is attained (Fig. 8B). Only one sexually mature male (testis smeared) had not developed a lengthened third claw. Male turtles become sexually mature when they reach a plastral length of approximately 7.0 cm, and the lengthening of tail and third claw of the forelimb are secondary sex characters.

Two adult females, 15.4 and 15.5 cm, were available to Cagle (1953:14). Of 35 females ranging from 4.1 to 17.0 cm, nine were considered sexually mature; the smallest one was 15.4 cm. All females (14) exceeding 12.5 cm were examined by dissection. Three, of four obtained in 1954 and dissected at the time of collection, had pigmented oviducts and were considered sexually mature; two (16.6 and 16.7 cm) had oviducal eggs, and the other (16.0 cm) had ovarian follicles 16.5 to 22.6 mm in diameter. The immature female (14.0 cm) captured in 1954 possessed unswollen oviducts 3 mm wide, and compact ovaries having the largest follicles 3 mm in diameter. Two immature females (13.1 and 14.9 cm) collected on June 30, 1949, and July 11, 1951, respectively, had ovaries that contained follicles 2 to 3 mm in diameter.

Eight females collected in the summer of 1955 (no exact date) were transported to the University of Kansas and not preserved there until early June, 1956. Of these, two females (12.7 and 15.3 cm), considered immature, had compact ovaries in which the largest oocytes were 2 mm in diameter; the oviducts, slightly pigmented posteriorly, were 2 to 3 mm wide in the smaller specimen, and 6 mm wide in the larger turtle. Six females (15.4 to 17.0 cm), considered sexually mature, had swollen convoluted oviducts 7 to 10 mm wide; the ovaries contained red bodies (corpora lutea or atretic follicles) not exceeding 4 mm in diameter, and the largest follicles were 3 to 5 mm in diameter. The posterior portions of the oviducts were nearly a uniform black. Although the definition of the size at sexual maturity is somewhat difficult to make by assaying the latter specimens, which are in a period of sexual inactivity, the two specimens, 14.9 cm (UOMZ 26911, immature) and 16.0 cm (UOMZ 27580, mature) indicate that females of *G. p. ouachitensis* in Lake Texoma are sexually mature when the plastron has attained a length of from 15.0 to 16.0 cm.

Eggs.—Only two of nine adult females contained eggs in their oviducts. One turtle, 16.6 cm and obtained on July 6, contained seven eggs (four in the left oviduct), which measured 22.2 to 23.8 (mean 23.2) mm in width, and 32.8 to 35.9 (mean 34.7) mm in length. A female (UOMZ 27581), 16.7 cm and captured on June 21, contained six oviducal eggs (four in the left oviduct), which measured 18.7 to 22.0 (mean 20.4) mm in width and 36.5 to 40.3 (mean 38.5) mm in length. The four eggs in the left oviduct from the turtle taken on June

21 were not turgid, but soft and crowded with creases in their walls; these eggs were noticeably more elongate and the measurements more variable than those of the other eggs. The two complements of oviducal eggs indicate a mean of 6.5.

Reproductive potential.—An analysis of the reproductive potential is limited to information obtained from an examination of three females. One, 16.6 cm and obtained on July 6, contained seven oviducal eggs. Her ovaries contained three follicles that ranged from 18.7 to 19.5 mm in diameter, and two, 14.4 to 15.4 mm; seven corpora lutea ranged from 8 to 9 mm in diameter, and six, 4 to 6 mm. Another female (UOMZ 27580), 16.0 cm and obtained on June 21, contained no oviducal eggs but the ovaries possessed five corpora lutea 8 mm in diameter and 26 enlarged follicles (10 were 16.5 to 22.6 mm, and 16 were 9.5 to 15.3 mm in diameter). The third specimen (UOMZ 27581), 16.7 cm and captured on June 21, contained six oviducal

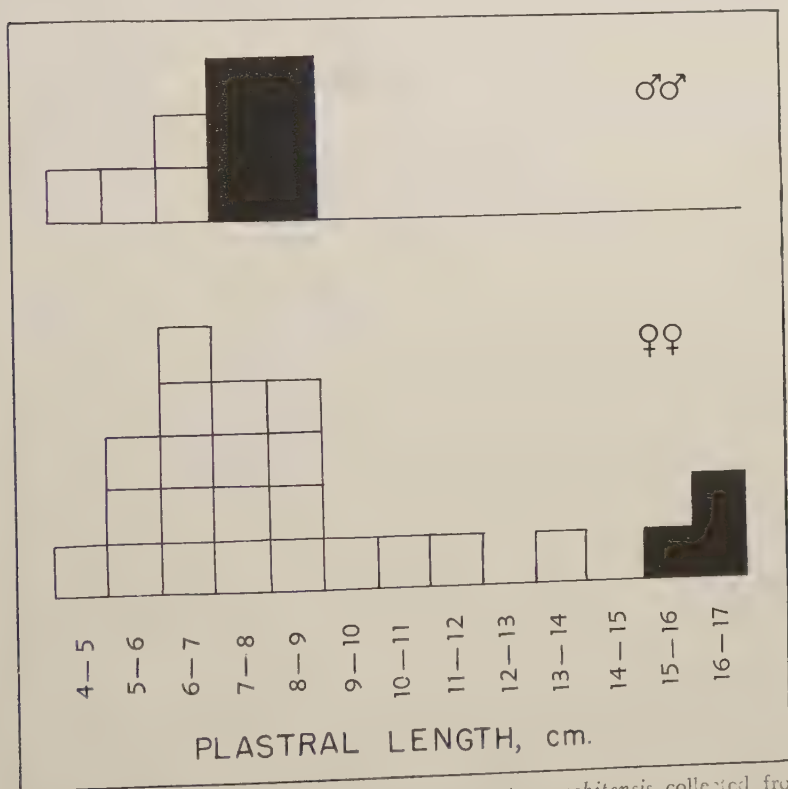


Fig. 7.—Size distribution of 34 *Graptemys p. ouachitensis* collected from June 13 through July 6, 1954. Open squares indicate immature individuals; solid squares indicate sexually mature individuals. Each square represents one specimen.

eggs. Her ovaries contained four follicles that ranged from 18.0 to 23.3 mm in diameter and five, 11.8 to 15.2 mm; six corpora lutea ranged from 8 to 9 mm in diameter, and eight, 4 to 7 mm.

The data suggest that, as in the Lake Texoma population of *P. s. elegans*, three clutches of eggs are laid in one season of sexual activity. This is evidenced by the possession of corpora lutea approximately 9 mm in diameter that are taken to represent the ovulation points of those eggs contained in the oviducts or those recently deposited (UOMZ 27580). The set of smaller-sized corpora lutea are indicative of an earlier clutch in the same season, and the enlarged groups of follicles (exceeding 15 mm in diameter) are suggestive of a subsequent egg complement to be deposited in the same reproductive season.

The ovaries of the females considered to be sexually inactive, contained follicles that did not exceed 5 mm in diameter and possibly corpora lutea not exceeding 4 mm in diameter, although the latter were not certainly distinguished from atretic follicles. A large corpus

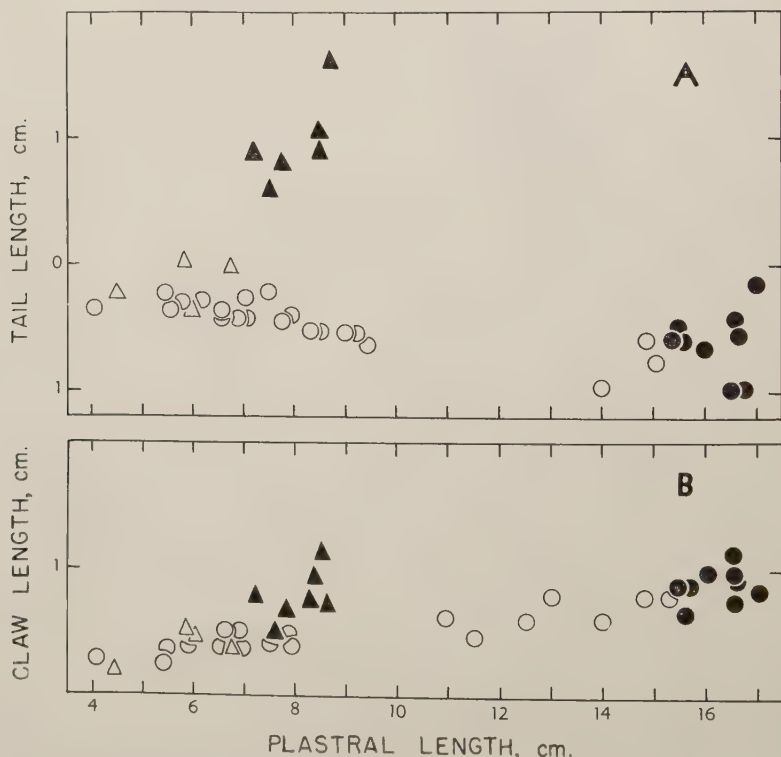


Fig. 8.—The relation of length of tail (A) and third claw of forelimb (B) to plastral length in *Graptemys p. ouachitensis*. Triangles indicate males and the circles females; solid symbols indicate sexually mature specimens, and open symbols immature specimens.

luteum (8 to 9 mm) is pale with red borders having a clearly-visible point of rupture, and is easily distinguished from an atretic follicle of the same or somewhat smaller size. The small size of the follicles in large sexually mature females, which were opened in early June at a time when much larger follicles are to be expected suggests that the environmental conditions to which the Kansas specimens were subjected in captivity were abnormal. Seemingly, ovarian follicles of a size at least 5 mm in diameter are contained in sexually inactive females. The abnormal conditions also may have prevented the complete regression of the corpora lutea; however, sexually inactive, females may contain corpora lutea approximately 4 mm in diameter.

It is assumed, then, that the largest set of follicles (exceeding 15 mm) are ovulated the same breeding season and corpora lutea of a size-group 4 to 7 mm represent ovulation points of an earlier clutch in the same reproductive season. Using only the most enlarged sets of follicles as a basis for an estimate of the reproductive potential, counts of 3, 10 and 4 indicate an average of 5.7 as compared with the realized oviducal egg count of 6.5.

The data suggest an annual reproductive capacity of at least 21 eggs (maximum of 7 per clutch; maximum of 3 clutches per season), and a realized annual reproductive capacity for each female of 19.5 eggs (mean of 6.5 per clutch; maximum of 3 clutches per season).

Growth.—Data derived from 28 turtles one to three years old indicate that measurement of growth rings are adequate for determining the length the plastron increases each year. This procedure assumes that, as in *Pseudemys s. elegans*, there is one annual growing season. Ideally a comparison of plastron lengths calculated from measurements of growth rings with those of hatchlings in which no growth has occurred is desirable. However, there is no difference in the mean plastral lengths of four hatchlings, which had not completed their first year of growth (2.8 to 3.1, mean 2.9 cm), and 24 turtles which either had completed their second or third or were in their fourth year of growth (2.2 to 3.4, mean 2.9 cm); measurements were calculated from growth rings of the femoral plate.

The calculated plastral length of 28 individuals at hatching was 2.2 to 3.4 (mean 2.9) cm, of which (two were not sexed) seven were males, 2.6 to 3.2 (mean 3.0) cm, and 19 were females, 2.2 to 3.4 (mean 2.9) cm. At the end of the first year of growth six males were 4.8 to 5.3 (mean 5.0) cm, and had increased 1.6 to 2.6 (mean 2.1) cm; 17 females were 3.6 to 6.0 (mean 5.0) cm, and had increased 0.7 to 3.5 (mean 2.0) cm. At the end of the second year of growth two males were 6.3 to 7.3 (mean 6.8) cm and had increased 1.1 to 2.4 (mean 1.8) cm; eight females were 6.0 to 8.1 (mean 7.1) cm, and had increased 1.4 to 2.6 (mean 2.0) cm. Of 23 turtles used in determining the growth rate, only one female, which had completed its third year of growth, still had the growth ring at hatching evident; this individual was 9.5 cm and increased 2.3 cm in its third year. A growth curve is plotted from the calculated plastral lengths

for these individuals (Fig. 9). Thus, some males become sexually mature in their second year (one, 7.3 cm). Assuming an average increase in females of 2.0 cm for each year (as indicated for the first two years), females do not become sexually mature until their sixth or seventh year. The rate of growth is approximately equal in both sexes during the first two years but more variable in females.

One hatchling, which had a calculated plastral length at hatching of 3.1 cm, increased only 0.5 cm when examined at the time of collection, June 16, 1954 (3.6 cm), whereas another having a calculated plastral length of 2.8 cm at hatching had increased 1.4 cm when

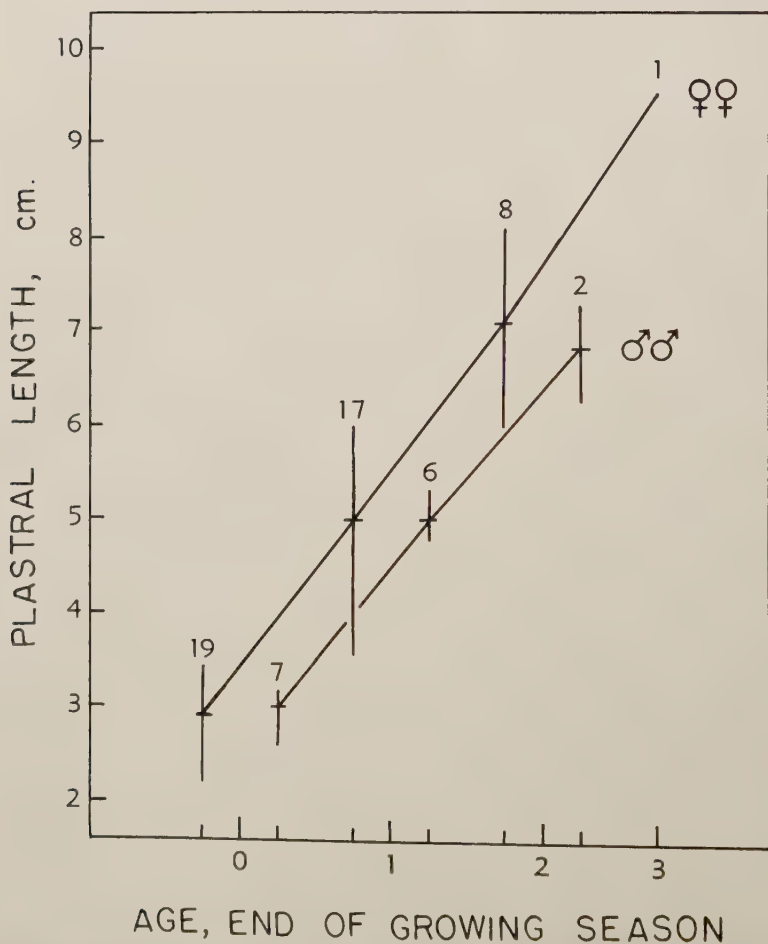


Fig. 9. Early growth of *Graptemys p. ouachitensis*. Vertical lines indicate the range in length of plastron; the diagonal lines connect the means. The figure above each line represents the number of specimens.

captured on June 17, 1954 (4.2 cm). This variation in rate of growth is also evident in females following their first year of growth (extremes in increase in length of plastron, 0.7 to 3.5 cm), and suggests the inclusion of individuals that are from clutches deposited at different times in the same breeding season. Presumably those turtles with small increments of increase are from clutches deposited late in the breeding season.

Five turtles that had the birth plate of the hatchling no longer evident, and whose age was therefore not definitely known, provide further data on the rate of growth. A sexually mature male (7.8 cm) when captured in the growing season of 1954, had calculated plastron lengths of 7.5, 7.1, 6.6 and 5.6 cm at the termination of the successive preceding growing season. Thus, there is a slowing of growth as the size at sexual maturity is attained; assuming the length of 5.6 cm to represent the size at the end of the first year of growth (see Fig. 8), this individual became sexually mature in its third year. Four immature females, 11.5, 13.1, 14.0 and 14.9 cm, showed variable and relatively rapid growth, the average increment of increase (combining those of different growing seasons) being 2.1 cm (extremes 0.9 to 3.7). The smallest increment, 0.9 cm, which occurred in the largest female (14.9 cm when obtained in the growing season of 1952), represented its last complete season of growth, and suggests the onset of sexual maturity. These data indicate that females grow rapidly prior to the attainment of sexual maturity (their first five to six years).

Food.—The stomach contents of eight immature *Graptemys* were analyzed qualitatively as completely as possible. Two males and six females, in which the length of the plastron ranged from 5.4 to 7.9 cm, were collected in the period June 17 to 19, inclusive. There was no indication that males and females differed in their food preferences.

A predominantly insectivorous diet was indicated in which midge larvae, ants and caddisworms (with cases of sand grains) were the most abundant items of food; small hemipterans were the next most frequent. Large portions of a bryozoan colony occurred in the stomach of one female. Small amounts of a filamentous alga and other plant fragments were perhaps ingested incidental to other food. The bulk of the contents in two specimens was composed of flesh, presumably fish, that was used for baiting the turtle traps. Numerous nematodes, four small flukes and a tapeworm from the intestines were also recorded. Other items identified include the remains of a crawfish, one cricket, one adult dragonfly and damselfly, one ephemeropteran naiad, one adult vespid wasp, two orb-weaver spiders, and coleopterans comprising three adult carabids, four dytiscid larvae and one elaterid larva.

The stomach of an adult female, 16.6 cm and drowned in a gill net on July 6, was gorged with grasshoppers. Another adult female, obtained in a fyke net on June 21, had an abundance of Bermuda grass (*Cynodon dactylon*) and fogwort (*Lippia incisa*) in the stomach.

The smaller individuals seem to prefer insects; this preference probably persists in the larger turtles. The feeding habits of this map turtle in Lake Texoma are perhaps best regarded as omnivorous in view of the presence of vegetable matter and carrion (fish). The presence of fish in the stomach contents suggests a purposeful entrance of the turtles into the traps. The diet is probably determined by the food supply available; this may vary seasonally and be largely influenced by the fluctuating water level.

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Additional New Species in the Genus *Priocnessus* Banks (Hymenoptera: Psammocharidae) with Photomicrographs of Genitalia of All the New Males

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ABSTRACT: Seven new species of the genus *Priocnessus* (Hymenoptera: Psammocharidae) are described. Known only from males are *P. evansi*, *P. ruficrus*, and *P. bicuspidus*. Descriptions based on females only include *P. hirsutus*, *P. nigropectus*, *P. tridentatus* and *P. grandis*. Both sexes are described for *P. spinosus*. The previously undescribed male of *P. hurdi* Dreisbach is treated. *P. cincticornis* (Cresson) and *P. orbiculatus* (Smith) are considered as distinct species and the males and females are redescribed. Photomicrographs of the genitalia of all new males and revised keys to the known neotropical species are presented.

In a previous paper (Dreisbach, 1960), I described seventeen new species of the genus *Priocnessus*, and presented keys to all known neotropical species.

A recently acquired collection contains seven undescribed species, males of *P. hurdi* previously known only from females, and additional individuals of *P. rubrus* and *P. niger*. This material was made available to me by Dr. H. E. Evans, who collected specimens on his recent trip to Mexico and who had secured other specimens from other collections.

In working up these specimens I have come to the conclusion that *P. cincticornis* (Cresson) and *P. orbiculatus* (Smith) are not the same species. Dr. H. K. Townes compared a male collected by myself in Mexico to Smith's type in the British Museum. The male matched the type of *P. orbiculatus* perfectly. This specimen has a black abdomen with large yellowish spots on the sides of the tergite while Cresson (1867) described *cincticornis* as having a yellowish-ferruginous abdomen; Cresson's type is a female and it does not seem logical that the male would have a black abdomen since males are normally more highly maculated and brighter colored than the females. The male of *orbiculatus* has the last three joints of antennae flattened and larger than the preceding joints. The posterior trochanter has a small ventral tooth at the apex. It is impossible to know whether the male of *cincticornis* would have these characters.

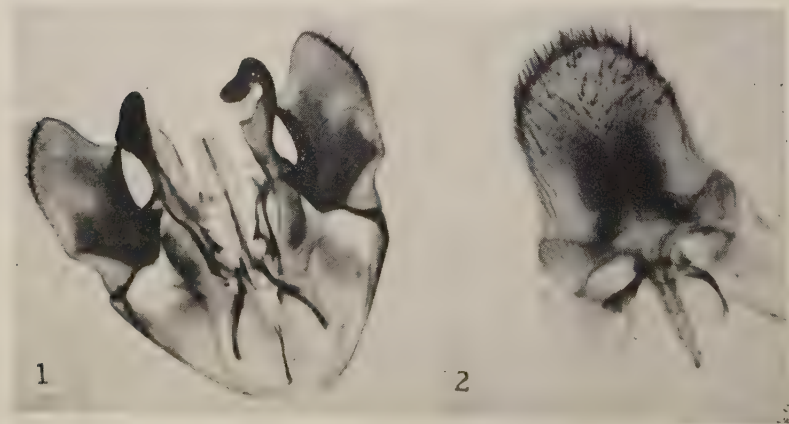
In the descriptions below, the numbers in parenthesis which follow the "lower" or "upper interocular distance" refer to the relative distance on the same scale as the ratio of the lengths of the first four antennal joints. All photomicrographs are from a magnification $\times 25$.

The designations for deposit of the type specimens in this paper are as follows: Am. Mus. = American Museum, New York City, New York; ANSP = Academy of Natural Sciences, Philadelphia, Pennsylvania; HAS = H. A. Scullen, Oregon State College, Corvallis, Oregon; CU = Cornell University, Ithaca, New York; PDH = Paul D. Hurd, Jr., Dept. of Entomology, University of California, Berkeley 4, California; RRD = R. R. Dreisbach, Midland, Michigan; and USNM = U. S. National Museum, Washington, D. C.

Priocnessus evansi n. sp.

Figs. 1 and 2

Holotype Male.—Insect mostly black, marked with color as noted; clypeus, face, front from inner orbits to antennae (narrowing to a point just opposite anterior ocellus), posterior orbits broadly, and middle of mandibles, whitish to yellowish; lower front corners of pronotum across lower edge and continuing upward and across posterior edge of pronotum, reddish yellow; all of the legs rufous beyond trochanters except last three joints of posterior tarsi, and blackish tips of coxae; most of trochanters also rufous; underside of antennae rufous, upper side black; tegula and base of wing rufous, about $3.0 \times$ the length of tegula; clypeus truncate in front; clypeus $3.2 \times$ as broad as long; middle interocular distance $0.58 \times$ the transfacial; head about $1.1 \times$ as broad as long; lower interocular distance about equal to the upper (105); vertex very slightly arched above eyes; lateral ocelli $1.5 \times$ as far from eyes as from each other; ratio of lengths of first four antennal joints is 50:12:60:60; pronotum almost transverse but slightly concave in center; the whole body with considerable white upright hair all over, giving a rough appearance; the ventral part of abdomen with considerable hair and last two sternites almost with a hair band; apex of all the tergites slightly rufous and last tergite yellowish white; wings yellowish hyaline with



Figs. 1 and 2.—*Priocnessus evansi*, n. sp. 1. Genitalia. 2. Subgenital plate.



Figs. 3 and 4.—*Priocnessus hurdi* Dreisbach. 3. Genitalia. 4. Subgenital plate.

veins yellow and a brown band across apical 0.7 of the second cubital cell extending backward almost to rear of third discoidal cell, apical 0.8 of wing beyond cells darkened about same amount; parameres of genitalia short and very broad; the subgenital plate, short, broad and with a characteristic darkened area sub-basally each side of midline; length head and thorax 5.3 mm, abdomen about 4.6 mm; length fore wing 9.9 mm, rear wing 7.6 mm; length genitalia 1.06 mm, width 0.93 mm; length of subgenital plate 1.26 mm, width 0.80 mm.

Type Locality.—Three miles NW. Cuernavaca, Morelos, Mex., 6500', May 29, 1959, H. E. Evans (USNM).

Priocnessus hurdi Dreisbach

Figs. 3 and 4

This species was described in the female sex only (Dreisbach, 1960).

Allotype Male.—Coloration almost exactly as in female except antenna is black dorsally beyond second joint, the first two joints completely rufous beneath also, but the rest of joints are brownish below; wings yellow with two faint bands as in female; subgenital plate much like *P. apache*, but basal triangle with ridges much more prominent and with two sub-basal transverse ridges at base of triangle; paramere with projection on outside near base, apicad of which is a shallow concavity and again a smaller projection; inside edge of volsellae of different shape than *apache*; length head and thorax 7.3 mm, abdomen 6.0 mm; length fore wing 11.7 mm, rear wing 9.3 mm; length genitalia 1.59 mm, width 1.3 mm; length subgenital plate 1.39 mm, width 0.86 mm.

Type Locality.—Four miles E. of Cuernavaca, Morelos, Mex., 6000', June 7, 1956, H. A. Scullen (HAS).



Figs. 5 and 6.—*Priocnessus ruficrus*, n. sp. 5. Genitalia. 6. Subgenital plate.

***Priocnessus ruficrus* n. sp.**

Figs. 5 and 6

Holotype Male.—Most of front, vertex, thorax except pronotum, abdomen and coxae, black; clypeus, face, sides of front from antennae to eyes narrowing on inner orbits opposite fore ocellus, all underside of antennae, all of apical half of joint 5 through basal half of joint 8, and last tergite, yellowish white; almost all of sides of pronotum to shoulders, a band covering apical half of pronotum, tegula and base of wings, scutellum, and all femora and tibiae, rufous or with more yellowish color; apices of abdominal tergites slightly rufous and about the apical 0.25 of sixth, yellowish; fore tarsal joints rufous, the last two pair basitarsi white, the two apical joints black, the joints in between yellowish white with apex and base darkened; clypeus with a narrow irregular hairless rim, widest in middle as a short broad tooth, about $2.4 \times$ as broad as long; head $1.15 \times$ as wide as long; middle interocular distance a little more than 0.50 the transfacial; lower and upper interocular distance equal (95); lateral ocelli 1.5 as far from eyes as each other; ratio of lengths of first four joints of antennae is 50:15:60:55; vertex in a slight curve above eyes; posterior margin of pronotum slightly angulate; wings hyaline, shining, yellowish in reflected light, veins yellow; fourth cubital cell slightly darkened; subgenital plate broadest at base rather deeply concave about middle; parameres very broad and short, no protuberances nor concavities on outside; volsellae with a long sharp pointed hook on side subapically; length head and thorax 6.5 mm, abdomen 6.5 mm, fore wing 10.5 mm, rear wing 7.9 mm; length genitalia 1.3 mm, width 1.0 mm; subgenital plate 1.4 mm, width 0.86 mm.

Type Locality.—Four miles E. Cuernavaca, Morelos, Mex., June 16, 1956, H. E. Evans (USNM).

Priocnessus bicuspidus n. sp.

Figs. 7 and 8

Holotype Male. Head mostly black and thorax almost entirely so, abdomen entirely rufous; face and clypeus yellowish on sides with a black longitudinal streak below and between antennae, which increases in width to apex where it occupies 0.33 of width of apex; sides of face yellowish from antennae to eyes decreasing in width on upper anterior orbits and ending in a point opposite anterior ocellus; posterior orbits same color whole length of eye; neck just behind head, the lower side of pronotum, a very narrow streak on posterior edge, and tegula, yellowish; a very short oculo-malar space black and mandible yellowish except the extreme apex is reddish; head with a few short hairs on vertex, but quite a few long yellowish hairs under head and around neck; face and clypeus with a few prostrate white hairs but not with a silvery appearance; however, the whole thorax (as well as coxae, more or less) sericeous with a rough appearance due to considerable upright hair; pronotum with hardly any dorsal surface, propodeum short, in a smooth slope; wings hyaline, slightly yellowish, evenly colored, no trace of dark clouds; veins yellow; in fore wings basal and transverse much displaced, more than length of transverse; in rear wings subdiscoidal barely apicad of cubitus; coxae black above rufous beneath; trochanters and all of rest of legs rufous; subgenital plate characterized by two small sub-basal teeth near each side, the area between them bare, the sides barely concave near base; parameres narrow for the genus, with two small protuberances on outside in basal half, with a very shallow concavity between them; volsellae with tips very short and blunt; length head and thorax 5.3 mm, abdomen 5.3 mm, fore wings 9.3 mm, rear



Figs. 7 and 8.—*Priocnessus bicuspidus*, n. sp. 7. Genitalia. 8 Subgenital plate.

wings 6.6 mm; length genitalia 1.3? mm, width 1.0? mm; subgenital plate 1.25 mm, width 0.6 mm.

Type Locality.—Four miles E. Cuernavaca, Morelos, Mex., 6000', June 29, 1959, H. E. Evans (USNM).

Paratype Males.—One same data (RRD); one same locality, date, June 20, 1959 (CU).

***Priocnessus hirsutus* n. sp.**

Holotype Female.—Head, thorax, abdomen and legs completely black, except apex of mandible is reddish; antennae black except the joints 5-7 are yellowish white dorsally and a trace of yellowish color on underside of one or two joints at each end of the three joints; the head, thorax, and coxae very hairy, with almost shaggy black hair; femora with short hair below; abdomen hairy on last two segments; body a glossy coal black with a very faint bluish tint; the apex of clypeus with three prominent teeth, the two outside ones rather sharp, the middle one blunt, the distance between outside edge of teeth almost $0.5 \times$ the width of clypeus at base; the edge between middle tooth and each side of outer tooth slightly concave; clypeus not raised above mouth parts as much as usual; clypeus $2.0 \times$ as broad as long; head a little more than $1.1 \times$ as broad as long; middle interocular distance a little more than $0.50 \times$ the transfacial; lower interocular distance (90) equal to the upper; lateral ocelli almost $3.0 \times$ as far from eyes as each others, ratio of lengths of first four antennal joints is 60:20:80:80; from in front vertex almost level with eyes; posterior edge of pronotum very slightly angulate; wings bright yellow with a strongly contrasting dark tip covering the outer half of membrane beyond the cells; basal vein very much basad of transverse, more than the length of the latter; in rear wings subdiscoidal and cubitus practically interstitial, the subdiscoidal vein slightly apicad; first and second recurrent veins received in the middle by second and third cubital cells; a row of about 8 teeth on inner edge of posterior tibiae with a row of small spines on outer edge set part way between them and opposite them, the shiny hairless surface between them narrowed at each tooth; length head and thorax 5.3 mm, abdomen 4.9 mm, fore wing 9.9 mm, rear wing 7.3 mm.

Type Locality.—Amecameca, Morelos, Mex., 8000', August 17, 1956, R. and K. Dreisbach (USNM).

***Priocnessus nigropectus* n. sp.**

Holotype Female.—Most of head, all of thorax and most of abdomen black; edge of face from base of clypeus and anterior orbits to fore ocellus and a spot behind top of eye, yellowish; a small yellowish spot on each side of first tergite, a large one on each side of second tergite, and smaller spots on each side of third and fourth tergites; all coxae, trochanters, basal 0.75 of fore femora and basal 0.25 of last two pair of femora, black; rest of legs rufous except

apical one or two joints of tarsi; on last pair tarsi the extreme base of second, third and fourth joints is black; considerable long yellow hair on head, thorax and abdomen; face and clypeus and especially the thorax with a slightly golden, prostrate, glistening pubescence; clypeus with four teeth on middle of apex, the outer two slightly pointed, the middle two very broad, the space between the teeth concave; the apical part bearing the teeth only $0.5 \times$ as wide as clypeus at base; the edge bearing the teeth hairless and polished, this area $0.3 \times$ as long as length of clypeus; clypeus $1.35 \times$ as broad as long; head about $1.25 \times$ as broad as long; middle interocular distance a little more than $0.5 \times$ as long as transfacial; lower interocular distance (95) equal to the upper; ratio of lengths of first four antennal joints is 50:18:90:80; lateral ocelli almost $3.0 \times$ as far from eyes as from each other; antennae underneath and apex of first joint above and basal 0.6 of third joint above, rufous, remainder, brown to black; vertex straight across, same elevation as eyes; pronotum on posterior edge very slightly angled; wings yellowish hyaline, veins yellow: basal and transverse veins about as far apart as length of the transverse, and in rear wings subdiscoidal, very slightly apicad of cubitus; the first recurrent vein meets second cubital slightly beyond middle, and the second meets third cubital cell slightly beyond basal third; about 7 broad oblique teeth on inner edge of posterior tibiae, with a strong sharp spine behind them that extends about the length of teeth beyond them; an outer row of spines; the space between teeth shining, and with some long hairs; length head and thorax 6.0 mm, abdomen 6.3 mm, fore wing 10.6 mm, rear wing 7.0 mm.

Type Locality.—Mexico (ANSP).

Priocnessus tridentatus n. sp.

Holotype Female.—Head, thorax and abdomen black maculated with yellowish white; face and clypeus and inner orbits to lateral ocelli yellowish white, except for a black spot on face just below antennae continuing as a black blotch in middle of clypeus (extending about half way to apex); the color on anterior orbits broad, not pointed at apex; two yellow spots just above and continuous to antennae, and the posterior orbits with a short yellow band at base and apex of eyes; a large spot at outer lower front corners of pronotum extending backward along lower edge, continuing upward and across the posterior edge of pronotum as a wide band $0.5 \times$ as wide as length of pronotum, irregular in front, a spot on posterior middle of mesonotum, on scutellum, postscutellum, a large spot on mesopleura just above second pair of coxae, a triangular spot under rear wing, a spot just above posterior coxae, on posterior outer corners of propodeum, a large somewhat irregular spot on each side of first four tergites (here and there with some rufous), a spot on each side of second sternite, apex of fore coxae, and part of dorsal surface of last two pairs of coxae, yellowish white; antennae rufous beneath.

black above; coxae black except as noted, trochanters black, yellowish at apex; femora and all the rest of legs rufous, except apical tarsal joint is dark; considerable long hair over apex of abdomen, last tergite with very dark rufous hair; clypeus projects at outer front corners into large broad blunt teeth, a much smaller middle tooth, the whole apical margin inset between the two outer teeth and slightly concave on each side of middle, the very wide front margin brownish transparent; mandibles tricolored, black at base, yellow in middle, and reddish at apex; clypeus much raised above mouth parts, $2.0 \times$ as broad as long; middle interocular distance slightly more than $0.5 \times$ the transfacial; head $1.2 \times$ as broad as long; lower interocular distance (160) $1.3 \times$ the upper; lateral ocelli $2.0 \times$ as far from eyes as from each other; ratio of lengths of first four antennal joints is 60:20:110:80; vertex level with top of eyes; posterior edge of pronotum only slightly concave in center, almost transverse; wings hyaline, yellowish, veins yellow, apical third of space beyond cells only very slightly darker; basal and transverse veins separated by more than length of transverse, and in rear wings subdiscoidal barely apicad of cubitus; first and second recurrent veins in fore wings received by second and third cubital cells at about apical 0.4 and about basal 0.4, respectively; teeth on dorsal surface of posterior tibia about like those in *P. nigropectus* but teeth are placed more nearly at a right angle to length, the teeth not so large and spines on outer edge are larger and have small teeth at their base; length of head and thorax 6.6 mm, abdomen 5.2 mm, fore wing 13.3 mm, rear wing 9.2 mm.

Type Locality.—Four miles W. of El Cercado, N. L., Mex., VI-6-1951, P. D. Hurd (PDH).

Priocnessus spinosus n. sp.

Figs. 9 and 10

Holotype Male.—Head largely black, thorax almost entirely black; abdomen rufous except for basal half of ventral and dorsal surface of first segment, and line on base of second tergite; about 0.67 of sides of clypeus, face from antennae to eyes, broad anterior orbits which narrow to an obtuse point opposite the fore ocellus, a spot behind top of eyes, upper edge of mandible, a ring almost all way around 5th and 6th antennal joints and apex of fore coxae on inside, yellowish; most of ventral surface of coxae and trochanters and all legs beyond trochanters except about the last two tarsal joints, rufous; the bases of third and fourth tarsal joints of last pair of legs, black; antennae mostly rufous ventrally beyond second joint and black on dorsal edge; face and clypeus mostly with upright yellowish hair; slightly on front and the whole thorax with golden prostrate pubescence; clypeus raised very high in middle, deeply excavated and with a small tooth in middle in front; a row of setae in middle of 5, 6 and 7th antennal joints; clypeus $2.75 \times$ as broad as long in middle; middle interocular distance equal to $0.50 \times$ the



Figs. 9 and 10.—*Priocnessus spinosus*, n. sp. 9. Genitalia. 10. Subgenital plate.

transfacial; head $1.14 \times$ as broad as long; lower interocular distance (125) $1.25 \times$ as long as the upper; lateral ocelli $1.5 \times$ as far from eyes as from each other; ratio of lengths of first four antennal joints is 65:20:100:100; posterior edge of pronotum slightly concave in middle; wings brownish hyaline; yellowish in transmitted light; posterior trochanter with a strong blunt, short, spine on apex on inside (hence name); subgenital plate rectangular with a broad flat slightly raised triangular (open at apex and as seen before dissection) area; a slight raised ridge near each side sub-basally, which has a small tooth at base; paramere with a large projection on outside at base and one on inside near middle; length of head and thorax 6.6 mm, abdomen 5.3? mm, fore wing 11.9 mm, rear wing 8.9 mm; length genitalia 1.7 mm, width 1.2 mm; length, subgenital plate 1.52 mm, width 0.86 mm. Mexico.

Type Locality.—San Cristobal, Casa, Chiap., Mex., 7500', May 2, 1959, H. E. Evans (USNM).

Paratype Male.—Same data except date April 26, 1959 (RRD).

Allotype Female.—Most of head, all of thorax, extreme base of first abdominal segment, all of antennae, except apex of third and all of fourth and fifth joints, all coxae and trochanters except apex, lower basal half of mandible, and last two joints of all tarsal joints, black; about basal 0.5 of sides of thorax, face to antennae, broad anterior orbits to fore ocellus, apex of third and all of fourth and fifth antennal joints, apex of coxae, yellowish and basal half or more of mandibles, yellowish; apex and more or less underside of trochanters, all the rest of legs, except two apical joints and abdomen, rufous; clypeus black across front, grooved back of front, a flange on outer fore corners, hardly a tooth on front but the apex irregular;

clypeus about $2.3 \times$ as broad as long; head $1.2 \times$ as broad as long, middle interocular distance $0.56 \times$ the transfacial; lower interocular distance $1.40 \times$ the upper; lateral ocelli $2.0 \times$ as far from eyes as from each other; ratio of lengths of first four antennal joints is 70:25:120:90; vertex straight across from eyes; posterior border of pronotum slightly arcuate; wings clear, but yellowish in reflected light; tegula and veins yellow except subcostal vein and vein back of it black from base to basal vein; about 7 large, narrow, flat, oblique teeth on dorsal surface of posterior tibiae, much smaller teeth on inside edge; length of head and thorax 7.3 mm, abdomen 6.0 mm, fore wing 12.2 mm, rear wing 7.9 mm. Mexico.

Type Locality.—San Cristobal I. Casa, Chiap., Mexico, April 26, 1959, 7500', H. E. Evans (USNM).

Paratype Females.—Two. Four miles E. of Cuernavaca, Morelos, Mexico, 8000', June 23, 1959, H. E. Evans (RRD) (CU).

***Priocnessus grandis* n. sp.**

Holotype Female.—Body a glossy, shining black; a very faint reddish line on anterior orbits from clypeus to fore ocellus; the first five joints of antennae black the last seven yellow; the legs have a slight rufous cast about six very long hairs extending forward from front of clypeus, a great many under the mouth parts, a few on posterior orbits, above and below on fore coxae a few under fore femora, and scattered hair on the sternites; clypeus truncate in front, $2.25 \times$ as broad as long; head about $1.1 \times$ as broad as long; the middle interocular distance $0.5 \times$ the transfacial distance; the lower interocular distance $1.3 \times$ the upper; thus the eyes strongly converging above; the ocelli very large, less than their diameter part, and the lateral ones slightly nearer the eyes than to each other; ratio of lengths of first four antennal joints is 80:30:130:80; third antennal joint is $1.3 \times$ the upper interocular distance; pronotum very short, slightly angulate on its posterior border; propodeum in a smooth curve, en-



Figs. 11 and 12.—*Priocnessus cincticornis* (Cresson). 11. Genitalia.
12. Subgenital plate.

tirely free of upright hairs; wings a dark yellowish; the basal vein basad of the transverse vein by the length of the latter; the first recurrent vein meets the first cubital cell almost at apical fourth, and the second recurrent vein meets the third cubital cell before the middle; in the rear wings the subdiscoidal vein is apicad of the cubitus by about the thickness of a vein; length of head and thorax 9.2 mm, abdomen 9.8 mm, fore wing 15.2 mm, rear wing 11.0 mm.

Type Locality.—Rio U Cayali, Peru, Dec. 2-23, F. 6178 acc. 33591, H. Bassler (Am. Mus.).

Priocnessus cincticornis (Cresson)

Figs. 11 and 12

Male.—Abdomen completely rufous except for the basal half of first tergite and basal three quarters of the first sternite; a very slight tooth on posterior trochanter; underside of first two antennal segments yellowish; a yellowish band on upper quarter of posterior orbits; subgenital plate with a short sub-basal ridge each side, subparallel and bearing outward directed hairs along its whole length; parameres rounded at apex; volsellae with a very broad hook at apex.

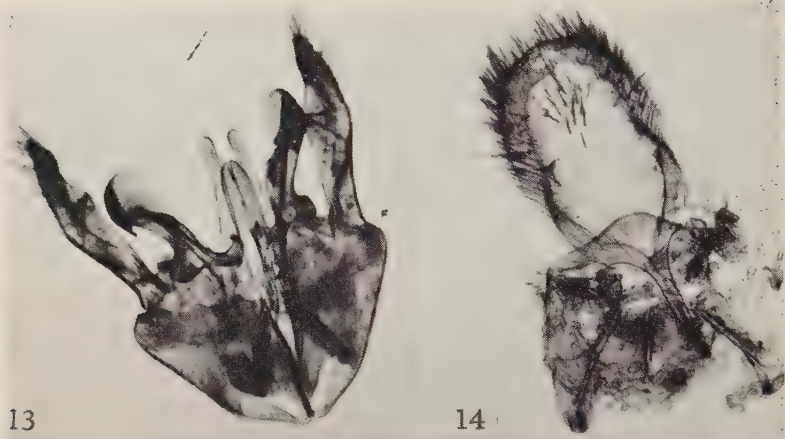
Female.—Abdomen yellowish ferruginous, except extreme bases of the first and second abdominal segments are black; the apical margins of the first and second abdominal segments and a stain on middle of second segment are fuscous; antennae black except the fourth and fifth joints are pale yellowish; apical abdominal segment is clothed with a golden pubescence. Mexico.

Priocnessus orbiculatus (Smith)

Figs. 13 and 14

Male.—Abdomen mostly black, with large yellowish spots edged with rufous on each side of the first four tergites; last tergite rufous; a plainly evident tooth at the apex on the underside of hind trochanter; underside of first antennal joint yellowish tinged with rufous; a yellowish band on the whole length of posterior orbits, except subapically; a good sized tooth in middle of apical edge of clypeus; last three joints of antennae distorted, flattened, larger than the preceding joints (do not know about this character for *P. cincticornis* as the joints beyond the fifth are lost); subgenital plate more strongly raised on basal dorsal surface, the elevation of sides bounded by a slightly curved ridge, bearing outward directed hairs only on apical half; parameres of genitalia more pointed at apex and volsellae with only a very short hook at apex. Mexico and Cuba.

Female.—Abdomen black and yellowish tinged with rufous; large yellowish spots, with rufous edges, on the sides of first three tergites; apex of abdomen rufous; sixth and seventh antennal joints white with a dark stripe; antennae yellow beneath; wings slightly darker beneath. Mexico.



Figs. 13 and 14.—*Priocnessus orbiculatus* (Smith). 13. Genitalia.
14. Subgenital plate.

REVISED KEYS TO THE NEOTROPICAL SPECIES

KEY TO FEMALES

1. White or yellow maculations on the thorax (*not* glittering spots of pubescence), head also well maculated, abdomen black with a great deal of yellow or completely rufous; wings white hyaline or slightly to strongly yellowish hyaline 2
1. No maculations on thorax but patches of silvery or golden pubescence may seem like maculations; wings generally strongly fuscous, yellowish, or reddish, in only about two species are wings yellowish hyaline 5
2. Clypeus with either one or three teeth on apical margin; abdomen black on dorsal surface (except dorsal surface of *first* tergite may be mostly yellow) maculated with yellowish spots on side 3
2. Clypeus with a small tooth on middle margin, margin each side concave; abdomen black, most of dorsal surface of first tergite yellow, two very large spots on sides of second tergite and two smaller ones on sides of third tergite, reddish yellow; first three joints antennae reddish, the rest black above, brown beneath; mandibles (except black apex) all clypeus, all face, front and broad anterior orbits to vertex, yellowish white, except a black streak in middle of front; posterior orbits all yellowish white; most of pronotum, a broad spot on mesonotum, band across scutellum, middle and posterior edge of postscutellum, a large spot above middle coxæ, smaller one under rear wing, the outer posterior corners of propodeum, and a spot above rear coxæ, yellowish white. Costa Rica.....
.....*flavidus* Dreisbach
3. Clypeus almost truncate in front; abdomen almost completely rufous on dorsal surface, base of first tergite is black and may have a yellow spot on base of first and sides of second tergite; rather broad anterior orbits, a spot on upper posterior orbits, a spot on posterior middle of *meso-*

- notum*, dorsal surface of scutellum, and postscutellum, yellow or yellow with some reddish 4
3. Clypeus with three teeth on apical margin; first tergite black with a yellow spot each side; a spot on each side of tergites 1-4, yellowish whole antennae black above yellowish beneath; mandibles tricolored, black at base, yellow in middle, and reddish at apex; pronotum with more black than in *flavidus*. Mexico. *tridentatus* n. sp.
4. Antennae with first five and a half joints and last three and one half joints black, joints in between yellow; mandibles except apex, clypeus (except black spot in middle), posterior edge of pronotum (except in middle) extending downward and covering tubercle, a large spot just above middle coxae, a large spot under rear wing, a large spot on outer posterior corners of propodeum continuing on outer corner of rim, and ventral surface of fore and middle coxae, white; fore tibiae black and white, posterior femora and tibiae, red; fore tarsi, middle tibiae and tarsi and last joint of posterior femora and tibiae, red; fore tarsi, middle tibiae and tarsi and last joint of posterior tarsi black; ventral surface of abdomen reddish suffused with black; wings almost hyaline. Brazil. *tricoloratus* Dreisbach
4. Antennae with first seven joints reddish (dorsal surface blackish), the rest black; mandibles (except base and apex), all of clypeus, lower side edge of pronotum, and legs beyond femora, reddish; broad posterior border of pronotum yellow with a reddish front edge; coxae, trochanters, and about basal half of femora black; abdomen with base of first tergite black and yellow and a yellow spot each side of second tergite; ventral surface of abdomen black with second and third ventrites suffused with yellow; wings with fore half of fore wing deep yellowish brown, the rear half and rear wing much lighter colored. Mexico. *anomalus* Dreisbach
5. Face and front densely bright golden pubescent, also some golden pubescence on thorax and abdomen 8
5. Face and front and abdomen without dense golden pubescence; thorax may have slightly golden pubescence, if so the antennae are yellow beneath and posterior orbits have a yellowish band 8
6. Face and front, densely golden pubescent, some on thorax but none on abdomen; posterior three fourths of pronotum a deep red, with silvery pubescence which appears slightly golden in reflected light; mesonotum and scutellum a deep red with no pubescence; a broad spot above middle coxae, the outer posterior corners of propodeum and the anterior corners of propodeum with brilliant shining silvery (slightly golden) appressed pubescence; the fore part of fore wing back to rear edge of second discoidal cell and covering cubital cells and fore edge of third discoidal and extending to wing tip, a deep brown, the rear of wing and all of rear wing hyaline; the contrast very prominent; exposed part of mentum and fore edge of clypeus red, the latter not much raised above mouth and concave on fore margin; abdomen red, legs black to about middle of femora then reddish; first five joints antennae reddish, last seven black. Mexico. *aureus* Dreisbach
6. Face, head and thorax densely covered with golden pile and prostrate pubescence; head and thorax black, but head with considerable yellowish color; coxae and trochanters black with apex yellowish; clypeus broadly yellow laterally and anterior orbits yellowish; pronotum black 7

7. Abdomen black and yellowish tinged with rufous; large yellowish spots on sides of first three tergites with rufous edges, apex of abdomen rufous; sixth and seventh antennal joints white with a dark stripe; antennae yellow underneath; wings slightly darker at tip. Mexico. *orbiculatus* Smith
7. Abdomen yellowish ferruginous, except extreme base of abdomen and of the second segment black and apical margin of first and second segments and a stain on middle of second segment, fuscous; antennae black, except the fourth and fifth joints are pale yellowish; apical segment clothed with a golden pubescence. *cincticornis* Cresson
8. Insect completely rufous except for sternum of thorax, tips of mandibles some sutures on thorax and base of first tergite, are black, *and* wings deep fuliginous or banded; or body completely rufous with black as above *and* wings light yellow and banded; pronotum angulate behind. 9
8. Insect not completely rufous and wings not fuliginous or banded 11
9. Insect rufous with deeply fuliginous wings; clypeus much raised above mouth parts, an indication of a tooth in front margin and concave each side of it; first two joints of antennae reddish, last 10 joints yellowish or black underneath, black on dorsal surface; first recurrent vein received by second cubital at apical third. Mexico. *rubrus* Dreisbach
9. Wings banded, with a dark band over basal veins, one over base of marginal cell and backward to rear of wing, and one on apex of wing beyond third cubital cell; wings yellowish between the bands 10
10. Insect rufous all over; only with very little black color on dorsal part of base of propodeum; no hairs on femora and no hairs on head or dorsum of thorax; head slightly longer than broad (42:40); clypeus about 2.3 × as broad as long; ratio of lengths of third and fourth antennal joints is 18:16; upper interocular distance slightly less than lower (20:22); a broad dark band over basal and transverse veins, a second one from base of marginal cell through all of second cubital and base of third cubital and across apical three fourths of third discoidal cell; clypeus hardly raised, truncate and with a slight rim; first two joints antennae reddish, rest brown beneath and black above; first recurrent vein received by second cubital cell just before middle. U.S. and Mexico. *apache* Banks
10. Insect not rufous all over, at least ventral surface of thorax black; head broader than long; ratios of various measurements different than in *apache*; apex of propodeum as well as sutures on side of thorax black, more black on base of propodeum, black upright hair on front, vertex and dorsal surface of scutellum and postscutellum, hair on rest of body yellow; first two joints of antennae red above and below, rest of dorsal surface deep black or with the fifth and sixth joints yellow *hurdi* Dreisbach
11. Body all black, at most with a slight reddish streak on anterior orbits; wings light yellow 12
11. Body not all black, either with maculations or some red color; wings generally more hyaline 18
12. Antennae, except tips, legs, and tip of abdomen fulvous; body fusco-ferruginous; wings yellowish hyaline; apex of fore wings fuscous and a cloud between the middle and apex fuscous. Cuba *nubeculatus* Cresson
12. Antennae wholly black, or with basal joints to four or six yellowish and rest of antennae black; no band in fore wings 13

19. Head and thorax with slight golden pubescence; head black with yellow maculations, thorax black (neck may have yellow streak) with yellow, appressed pile; abdomen ferruginous or black with yellow and reddish maculations; wings flavo-hyaline, veins yellowish20
19. Head and thorax without golden pile, thorax and abdomen different.....21
20. Abdomen black, maculated as follows; two preapical spots on sides of first tergite, a large spot each side in middle of second tergite, two smaller linear spots on sides of third tergite, two spots about same size on sides of fourth tergite, yellow; apices of first four tergites rufous and the last two segments entirely rufous; the first four sternites with posterior edges rufous; most of mandibles, a large spot each side of clypeus, face, broad anterior orbits, a spot in upper posterior orbits and narrow line on neck, yellow; antennae entirely black of slightly rufous near base; coxae and trochanters black; legs reddish except last joint fore tarsi, last three joints middle tarsi, and last four joints of posterior tarsi black or blackish; clypeus with a small tooth in middle, slightly concave each side, a narrow rim on apex; large teeth on posterior tibiae. Costa Rica
..... *ornamentatus* Dreisbach
20. No spots on tergites and sternites as in *ornamentatus* except apices of sternites are slightly rufous; mandibles black, except reddish apex, clypeus and face black; anterior orbits narrowly yellow and a spot on upper posterior orbits; thorax entirely black; basal 0.75 of fore femora, basal 0.5 of middle femora and basal 0.4 of posterior femora black; rest of legs rufous except apical joints of all tarsi are black; two teeth, broad and blunt, on outer edge of clypeus and two broad projections between them indicating four teeth, the edge between each two teeth slightly concave; seven narrow, oblique teeth on dorsal surface of posterior tibiae. Mexico. *nigropectus* n. sp.
21. Antennae with the first two joints and base of third red, rest black; wings a strong reddish yellow, veins strongly reddish except subcosta is amber from base to slightly beyond basal vein; sides of face yellowish from base of antennae to eyes, the yellow color continuing on anterior orbits to the fore ocellus, almost as broad on front as on face; mandibles yellowish on basal half black on apical half; in certain lights, pubescence on face and thorax golden; apex of fore coxae yellow, all trochanters red; legs all red except the two apical tarsal joints; a large species 21.5 mm long. Peru. *semirufus* Dreisbach
21. First two and three fourths of third antennal joints black, apex of third, the fourth, fifth and basal three fourths of six white, rest black; wings hyaline, slightly dusky, veins yellowish in reflected light; face black, anterior orbits from antennae to just before antennae with a whitish line; basal 0.75 of mandibles black, a preapical red streak, the apex black; head and thorax completely black with silvery pubescence; all coxae and trochanters black; basal half of fore femora black, and base of last two pair black, rest of legs all reddish including apical tarsal joints; a smaller species, 13.4 mm. Mexico. *durangoensis* Dreisbach
22. Head, thorax and abdomen mostly black with white or yellow maculations23
22. The whole body yellowish or at least the abdomen rufous24
23. The sixth antennal joint entirely, the fourth broadly at apex, and the fifth at base, yellow, the rest of antennae black; mandibles (except at

- apex), clypeus broadly at side, inner orbits broadly, the outer orbits more narrowly at top and bottom, the edges of pronotum all around (except in middle in front) tegula, a mark in center of mesonotum, middle of scutellum, a mark on postscutellum, two marks on mesopleura behind (the lower one the longer), a mark on lower and anterior end of metapleura, and a large mark on sides of abdominal tergites, yellow; a tooth in middle of front edge of clypeus; ventral surface obscure yellow; wings hyaline, nerves black; head and thorax opaque. Panama. *neotropicalis* Cameron
23. Antennae completely black; mandibles black, clypeus black; anterior orbits narrowly, a spot back of eye on temple, a small spot on anterior corners of neck, preapical posterior border of pronotum (except in center), a spot on posterior center of mesonotum, a band on scutellum, a small spot under posterior wing, a larger spot above middle coxae, a spot on outer posterior corners of propodeum, spots on extreme sides of first four tergites, yellow; legs black, but middle and posterior tibiae yellowish on posterior edge, and some on sides, these parts and tarsi with golden colored spines; a tooth on fore margin of clypeus; head and thorax (particularly thorax) shining, fore part of pronotum and neck bare and shining. Mexico. *octomaculatus* Dreisbach
24. Whole body pale yellowish, pronotum angulate behind25
24. Head and thorax black or black and maculated, abdomen rufous26
25. Antennae pale on first and second joints, black beyond; head, thorax and abdomen reddish yellow, legs and palpi also, but tarsi darker; fore wings rather yellowish in the cells, veins dark and bordered with dark or smoky, broadly so at basal vein and a broad dark cloud over most of marginal cell and back into apical part of third discoidal cell, wing tip smoky, hind wing also yellowish, tip smoky; head, thorax, coxae, venter and three apical segments with rather long fine hair; some appressed golden hair on head; both recurrent veins meet the second and third cubital cell at about middle. West Indies. *monticolus* Banks
25. Antennae mostly pale yellowish, but last six joints pale brown; a dark stripe above antennae each side reaching up to ocelli; a narrow black line from eye to eye; mesonotum with a broad median black mark, not reaching behind border, each side a broad black stripe from wing base forward and connected on each other behind, thus leaving a pale U in middle; scutellum with a black spot in middle of base, black behind, postscutellum yellowish across frontal part; propodeum with a large black streak each side leaving only a narrow pale median line, the dark sides narrower behind; pleura entirely pale; wings mostly hyaline, fore wings with a pale brown costal streak beyond basal vein and covering marginal, first, second, and most of third cubital cells and beyond to wing tip. Colombia. *bequaerti* Banks
26. Head and thorax with pale yellow or creamy white spots; clypeus, a broad streak on anterior orbits not touching clypeus, a streak on posterior orbits, an elongate spot on each side of hind margin of pronotum and the lower margin broadly and almost touching side spot of hind margin, a median spot behind on mesonotum, a small spot on scutellum, a larger one on postscutellum; one on outer side of fore coxae and several on sides of thorax, pale yellow or creamy white; petiole of abdomen and fore femora black except rufous on tip; mid and hind femora, all of tibiae, and basal part of tarsi pale yellowish, last few tarsal joints jet

- black; antennae with six or six and one half joints jet black, five or four and one half creamy-white, the last joint brown; pronotum angulate behind. Trinidad. *ornatus* Banks
26. Thorax not maculated and otherwise not as above 27
27. Coxae, trochanters and femora, except apex, black; apex of femora and rest of legs reddish, except last two tarsal joints of fore legs and last three tarsal joints of middle and posterior legs, black; head and particularly the thorax strongly silvery sericeous with prostrate, glistening pubescence; clypeus slightly concave in front, with a rather broad, preapical rim, which forms a slight trough (concave), particularly on the side pieces; mandibles (except tip and lower edges), sides of face, rather broad anterior orbits to lateral ocelli, and a small spot on posterior orbits just below temples, white; antennae with first two and basal three fourths of third joints black, apex of third and joints four and five, and base of six underneath, white; third joint of antennae not as long as fourth; lower interocular distance 1.3 times the upper; thorax especially shaggy, long haired, hairs light colored. Panama, Colombia. *sericeus* Dreisbach
27. Legs all red except coxae and trochanters are black, and last tarsal joints are blackish; an indication of a broad tooth in middle of apical margin of clypeus and a preapical rim on clypeus; first two joints antennae black, apex of third and all of fourth and fifth bright yellow, rest of antennae black 28
28. Sides of clypeus at base, fairly wide anterior orbits from clypeus to lateral ocelli, a linear spot on posterior orbits just below temples, most of mandibles and all mentum, *reddish*; *pronotum deep red*; wings light yellow; teeth on posterior tibiae very small; length about 14.5 mm long. Ecuador. *caesius* Dreisbach
28. Sides of clypeus at base of about 0.75 of width, yellowish, the color narrowing toward apex so that at about middle of clypeus it covers about 0.4 of width, about 0.3 of apex black; face below antennae and a mark in middle of sides at base of clypeus black the rest yellow and the color continuing on anterior orbits broadly, to beyond fore ocellus; mentum black, and all of abdomen black; mandibles yellow on basal 0.5, dark on apical 0.5; large teeth on inner edge of dorsal surface of posterior tibiae, and fairly good sized teeth on outer edge, long scattered hairs between the teeth; length about 13.0 mm. Mexico. *spinus* n. sp.

KEY TO MALES

1. Clypeus entirely yellow or mostly yellow with a dark spot or band in middle 2
1. Clypeus with no yellow marks whatever; very narrow yellowish mark on anterior orbits in one case 10
2. Last trochanter with a strong tooth on apex of under side *and* abdomen red, legs red (including underside of coxae) except last two or three tarsal joints which are black; first two joints of antennae red, the rest black; head and thorax with golden prostrate pubescence spotted over most of surface; wings rather strongly fumous, yellowish; subgenital plate somewhat elevated, rectangular, with spines over apical sides and across apex; clypeus yellow with a large black spot in middle; mid and posterior tarsi black beyond basal joint. Peru and Colombia. *prominens* Banks

2. If a strong tooth on apex of hind trochanter, a black band lengthwise in middle of clypeus 3
3. Clypeus completely white 4
3. Clypeus white at sides, a longitudinal black band in middle 7
4. Wings hyaline without bands, only apex of wing darker; face entirely yellowish as well as most of pronotum; apical tergite whitish and apex of preceding tergite rufous; abdomen black; subgenital plate with base wider than apex and strongly restricted in width *above* middle of plate, dark colored; parameres very broad, short and with no protuberances on outsides. Mexico. *ruficrus* n. sp.
4. Wings with bands and hyaline between bands or the wings strongly darkened, so bands are not so evident; subgenital plate different 5
5. Wings very much darkened but with slightly stronger color over basal veins and cubital cells; thorax mostly rufous; coxae, trochanters and first two antennal joints rufous as well as abdomen; no protuberances on outside of trochanters near base; all femora rufous; size large 13.5 mm. Mexico. *hurdi* Dreisbach
5. Wings banded over basal veins (or not) and cubital cells, hyaline (brownish) between bands; apex of wing dark; coxae and trochanters black 6
6. Abdomen black, first two joints of antennae black above; thorax black; all femora rufous; no cloud over basal veins; subgenital plate more nearly rectangular with a sub-basal dark cloud each side near middle; parameres much broader and slightly concave on outside at base. Mexico. *evansi* n. sp.
6. Abdomen rufous; first two joints of antennae completely rufous; posterior femora mostly black; a cloud over basal veins; pronotum rufous and rest of thorax with some rufous; subgenital plate more ovoid not rectangular, with no dark cloud; parameres much narrower, straight on outside. U.S. and Mexico. *apache* Banks
7. Thorax and sometimes the head with golden pubescence; a small or a strong tooth on underside of hind trochanter at its tip; no prominent tooth sub-basally near the sides on subgenital plate, this is plainly visible without dissection; neck and pronotum black 8
7. Neither head nor thorax with golden pubescence, but pubescence is silvery but slightly yellowish in certain light; no trace of a tooth on posterior trochanter; a prominent tooth sub-basally near sides on ventral surface of subgenital plate near the sides, visible without dissection; neck with a white spot where it joins the head, and the lower side of pronotum yellowish. Mexico. *bicuspидatus* n. sp.
8. A strong thick obtuse tooth on apex of ventral side of hind trochanter; abdomen rufous, except basal half of first segment; golden pubescence strong on thorax; legs all rufous beyond trochanters except apical tarsal joints; a larger species. Mexico. *spinus* n. sp.
8. Either a small tooth or barely an indication of one; golden pubescence not so strong on thorax 9
9. Abdomen completely rufous except for about the basal 0.5 of first tergite and basal 0.75 of first sternite; a very slight tooth on posterior trochanter; underside of first two antennal joints yellowish; a yellowish

- band on upper 0.25 of posterior orbits; subgenital plate with a short sub-basal ridge each side, subparallel and bearing outward directed hairs its whole length; parameres and volsellae rounded at apex. Mexico. *cincticornis* (Cresson)
9. Abdomen mostly black, with large yellowish spots edged with rufous on each side of the first four tergites, last tergite rufous; a plainly evident tooth at apex on the underside of last trochanter; underside of first antennal joint yellowish tinged with rufous; a yellowish band on the whole length of posterior orbits, except subapically; a good sized tooth in middle of apical edge of clypeus; last three joints of antennae distorted, flattened, larger than preceding joints (do not know about *cincticornis* as joints beyond the fifth are last); subgenital plate more strongly raised on basal dorsal surface, the sides of elevation bounded by a slightly curved ridge, bearing outward directed hairs only on apical half; parameres more pointed on apex and volsellae truncate across apex, slightly emarginate. Mexico and Cuba. *orbiculatus* (Smith)
10. Narrow yellow lines on anterior orbits from base of clypeus or just above; clypeus with three teeth on front margin, middle one small triangular, the sides concave each side to the lateral broader teeth; clypeus much raised above mouth parts, strongly arched. 11
10. No marking on anterior orbits, body wholly black; clypeus *without* teeth, concave on front margin or almost truncate. 13
11. Antennae wholly black; wings reddish with contrasting black tip; subgenital plate elongate, gradually narrowing from base to broad obtuse apex; a few long hairs almost as long as width of plate on sides near apex and around apex; a raised hairless area, broad at base then gradually converging to apical fourth, sides above base subparallel; parameres of genitalia with a large concavity on outside near base. Mexico. *lineatus* Dreisbach
11. Antennae with some joints completely yellow; wings reddish with a black cloud in second cubital and third discoidal cell, or hyaline with black veins; subgenital plate shorter and ovate, or as long but sides concave just above base. 12
12. Antennal joints 5-8 completely yellow, joints 3, 4 and 9-11 yellow beneath, black on dorsal surface; linear impressions on joints 6-8; wings reddish yellow with a blackish cloud in second cubital and third discoidal cell; apex of wing blacker than in *lineatus* covering most of third discoidal cell; subgenital plate much shorter than in *lineatus*, ovate, triangular area shorter, not as broad; shorter hair on sides and around apex; parameres of genitalia short and broad, the outside edge straight without a large concavity. Mexico. *kayi* Dreisbach
12. Some of middle antennal joints yellow; wings hyaline with dark veins; subgenital elongate, with the sides just above base concave, a broad basal triangle which is open at apex, the prominent sides of triangle ending about middle of plate; parameres of genitalia much more slender and longer than in *kayi*. Panama. *neotropicalis* (Cameron)
13. Head and thorax with hair black, only slightly reddish in reflected light, no appressed reddish pubescence; clypeus hardly raised above mouth parts and truncate in front; eyes reach vertex; pronotum transverse behind; subdiscoidal vein of rear wing is interstitial with the cubitus; no teeth and only a very few small spines on posterior tibiae; subgenital

- plate concave on sides about middle, the upper half of plate semiorbicular, the raised portion at base wider than in next; size smaller about 13 mm long. Honduras. *hondurensis* Dreisbach
13. Head and thorax with reddish black hair and with appressed reddish pubescence; clypeus raised above mouth parts and concave on front margin; pronotum angulate behind; subdiscoidal vein in rear wings apicad of cubitus; small teeth and spines on dorsal surface of posterior tibiae; subgenital plate almost rectangular, only slightly concave on sides near middle, the upper half with sides parallel to close to apex; size larger about 15 mm. Mexico. *rogersi* Dreisbach

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Three New Species of the Genus *Entocythere* (Ostracoda, Cytheridae) from North and South Carolina¹

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ABSTRACT: Investigations on the ostracods epizoic on crayfishes has led to the discovery of three new species. A morphological treatment along with taxonomic consideration is accorded each of these new forms. The known range of each new species together with the host relationships is presented.

In studying commensal ostracods of the genus *Entocythere* Marshall (1903) of western North Carolina and northern South Carolina, three new species were encountered and are described herein. One of them is a member of the Columbia Group Rioja (1949) and the other two are distinctly related to members of the Runki Group Crawford (1959).

Insofar as is known, the members of this genus are all associated with crayfishes, and the determinations of the hosts of the three new species were made by Dr. Horton H. Hobbs, Jr. of the University of Virginia. These crayfishes have been deposited in his personal collection.

The methods utilized in this study were similar to those outlined by Crawford (1959:149).

*Entocythere clemsonella*², sp. nov.

Male.—Valve (Fig. 7) suboval in lateral aspect with the anterior and ventral margins smoothly rounded. Dorsal margin slightly arched along posterodorsal edge. Setae sparsely scattered on lateral surface of valve and irregularly dispersed along free margin. Eye located about one-sixth of valve length from anterior end. Valve size relatively constant as indicated by the measurements of 10 specimens from the type locality mounted in Hoyer's solution: length, 0.345 mm to 0.375 mm, average, 0.361 mm; height, 0.210 mm to 0.225 mm, average, 0.214 mm.

Antenna I with six podomeres, the basal one is longest and third from base shortest; three distal podomeres subequal in length. Diam-

¹ This study was made possible by a grant from the American Association for the Advancement of Science through the South Carolina Academy of Science.

² This species is named in honor of the late Thomas Green Clemson, distinguished diplomat, able mining engineer, active promoter of scientific education in the United States, and founder of Clemson A & M College.

eters of successive podomeres diminish regularly distally. One seta borne on apical end of both first and second podomeres with two on third. Antepenultimate podomere with six setae, penultimate devoid of setae, and ultimate with five terminal setae.

Antenna II (Fig. 1) with four podomeres; basal one bearing subapical antennal flagellum. Antepenultimate podomere little wider than long, with distal flexor margin bearing a heavy, feathered, spine-like seta. Penultimate podomere with two setae borne on apical flexor margin. Ultimate podomere apparently divided toward apical end and with heavy setae in notch on midflexor margin. Characteristic terminal claws borne on distal portion of ultimate podomere; dorsal claw stalked and prominently arched proximally with flattened distal surface bearing 10-12 teeth; middle claw short and toothed, and ventral claw arched distally with cluster of teeth on ventrodistal surface.

Mandible (Fig. 2) with protopodite bearing a row of six multicuspid teeth distally; the two proximal teeth with one or two cusps, the middle three with three cusps, and the distal tooth with five. Heavy seta borne in notch on convex surface of protopodite at level slightly proximal to proximal tooth. Respiratory plate with three setae. Palp consisting of four indistinct podomeres; basal one with long seta borne on distal flexor margin; short antepenultimate podomere without setae; penultimate podomere with two setae, one of which is borne in notch on midextensor margin, the other arising from apical end; and short ultimate podomere with three heavy setae on distal end.

Maxilla (Fig. 4) with protopodite bearing two terminal setae. Unsegmented palp with two apical setae, the ventral one being heavier. Conspicuous notch present on dorsal surface of palp. Respiratory plate with 15-20 plumose setae.

Copulatory complex (Fig. 5). The proximal portion of the base is subspatulate in shape, somewhat similar to that of *E. telmoecca* Crawford (1959). Attached to the proximal portion of the base are the dorsal and ventral fingers; the latter is more attenuated and longer than the former; the terminal spine of the former appears to be bifurcate. The distal portion of the base is long and narrow, the posterior margin bearing a concavity at its midlength. The anterior and posterior margins join to form an acute angle. The rami of the clasping apparatus (Fig. 3) form an angle of about 70 degrees. The flexor surface of the horizontal ramus bears three teeth on the distal half which decrease in prominence distally. The entire extensor margin of the horizontal ramus is smooth. Four prominent teeth are borne on the distal end of the horizontal ramus.

Female. The valve of the triunguis forms (Fig. 6) is suboval in lateral aspect with the ventral margin bearing a slight concavity just anterior to midlength. The dorsal and anterior margins are evenly rounded with the posterior one being slightly arched. The free margins of the valve are setiferous, and the lateral surface sparsely so. The

eye is located one-fifth of valve length from the anterior end. The measurement of 10 specimens from the type locality mounted in Hoyer's solution exhibit a range in length of 0.395 mm to 0.420 mm, with an average of 0.410 mm; in height the range is 0.240 mm to 0.270 mm, and averages 0.258 mm.

The second antenna of the triunguis female generally bears three terminal claws; however some specimens apparently have only two. The dorsal claw, bearing a few teeth on the distal end, is about two-thirds as long and more slender than the ventral claw. The very slender middle claw is two-thirds as long as the dorsal claw, and is without teeth on the distal end. The ventral claw is heavy and has 10-15 teeth on the ventrodiscal surface.

The valve of the biunguis female (Fig. 8), in lateral aspect, is oval, being slightly arched along the posterodorsal margin. It is slightly smaller than that of the triunguis form.

The genitalia of the triunguis female consists of a short, thick, heavily sclerotized, hollow tube (*pieza quitinosa femenina*), Rioja (1943:575) which is directed ventrad.

Type Locality.—Small, intermittent stream on S. C. Route 20 about 1.4 miles north of Abbeville, Abbeville County, South Carolina. The crayfish host here is *Cambarus latimanus* LeConte (1855). *E. internotalus* Crawford (1959) and *E. striophylax* Crawford (1959) were also found in collections from the type locality.

Disposition of Types.—The holotypic male, the allotypic (triunguis) female, the morphotypic (biunguis) female, and a dissected male paratype are deposited in the United States National Museum. Paratypes are in the collections of Drs. Horton H. Hobbs, Jr., Eugene N. Kozloff, and the author.

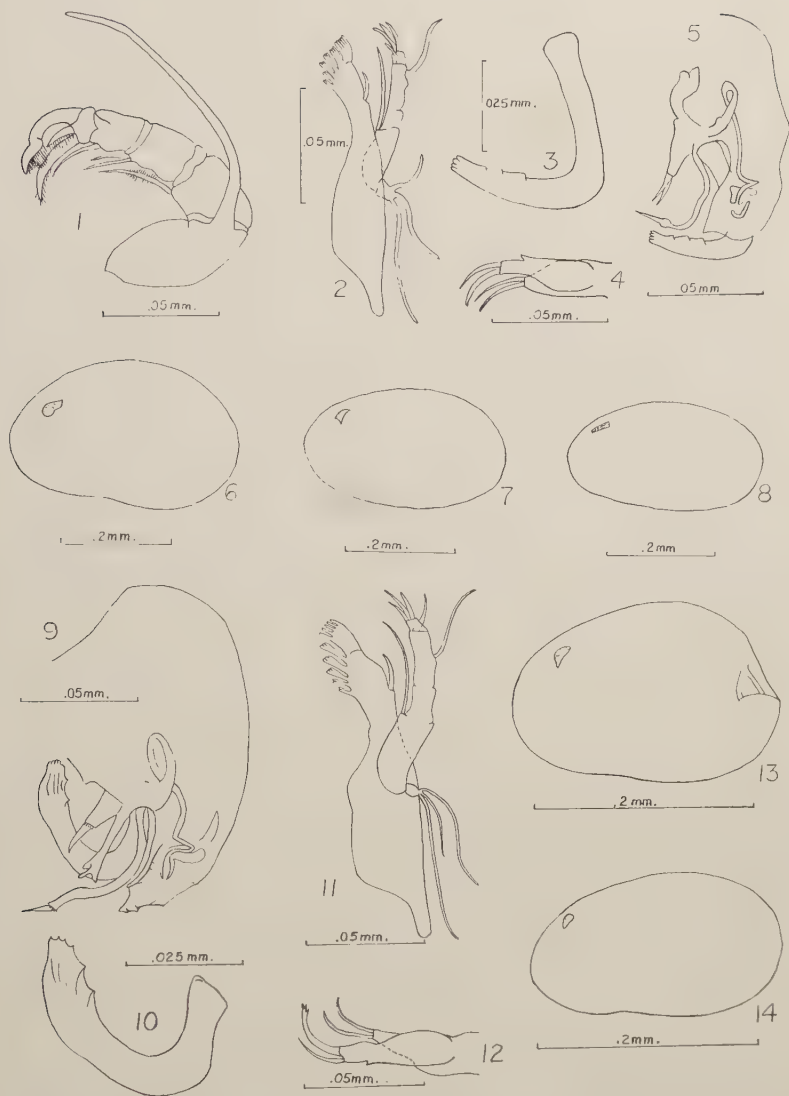
Range.—This species was found in two collections other than that from the type locality: (1) a tributary of Little River in Rock Eagle Park, Putnam County, Georgia, and (2) Skeleton Creek near Gaffney, Cherokee County, South Carolina.

Remarks.—This species seems to be closely related to *E. riojai* Hoff (1943) and *E. equicurva* Hoff (1944). There is a striking similarity in the clasping apparatus of this species to that of *E. riojai* although the proportionate lengths of the vertical and horizontal rami readily separate the two species; the vertical ramus is relatively longer in the latter. The character of the horizontal ramus of this species easily distinguishes it from that of *E. equicurva*. The C-shaped clasping apparatus definitely places *E. clemsonella* in the Columbia Group Rioja (1949).

*Entocythere leptophylax*³, sp. nov.

Male.—Valve (Fig. 14) subelliptical with anterior end narrower than posterior. Margins smoothly rounded except for slight concavity

³ This name is derived from Greek (leptos — narrow; phylax — guard) and refers to the narrow, thin, finger guard.



Figs. 1-8.—*Entocythere clemsonella* sp. nov. 1. Antenna II of male. 2. Mandible of male. 3. Clasper of male. 4. Maxilla of male. 5. Copulatory complex of male. 6. Lateral aspect of valve of triunguis female. 7. Lateral aspect of valve of male. 8. Lateral aspect of valve of biunguis female. Figs. 9-14.—*Entocythere leptophylax* sp. nov. 9. Copulatory complex of male. 10. Clasper of male. 11. Mandible of male. 12. Maxilla of male. 13. Lateral aspect of valve of triunguis female. 14. Lateral aspect of valve of male.

on ventral margin just anterior to midlength. Height greatest slightly posterior to midlength. Setae scattered along free margin of valve but more numerous on anterior end; lateral surface with few widely spaced setae. Eye located about one-sixth of valve length from anterior end. Valve size of ten specimens from type locality mounted in Hoyer's solution indicates a range in length from 0.435 mm to 0.465 mm, average, 0.450 mm; height, 0.240 mm to 0.290 mm, average, 0.273 mm.

Antenna I with six podomeres; the basal one is longest with second, third, and fourth subequal in length. Ultimate podomere about two-thirds as long as basal one. One seta borne on distal ends of first and second podomeres with two in corresponding position on third. Antepenultimate podomere with six long setae, penultimate devoid of setae, and ultimate with five terminal setae.

Antenna II with four podomeres; basal one devoid of setae but with a long, thin, antennal flagellum on apical end. Second podomere with feathered, spine-like seta on distal flexor margin. Penultimate podomere with two setae on distal flexor extremity. Ultimate podomere divided toward apical end; proximal portion bearing a seta on distal flexor margin. Distal portion of ultimate podomere with the three characteristic terminal claws: stalked dorsal claw arched proximally with flattened distal surface distinctly toothed; short, toothed, middle claw stalked; and ventral claw, the longest, bearing numerous teeth on distal portion of ventral margin.

Mandible (Fig. 11) with a row of six or seven multicuspid teeth borne on distal end of protopodite; proximal tooth bicuspid, middle three tricuspid, and prominent distal tooth with five cusps. Convex surface of protopodite with heavy seta at level of proximal tooth. Respiratory plate with three setae, two relatively long and subequal in length, and one about one-half as long as others. Mandibular palp with four indistinct podomeres; basal one with long seta borne on distal flexor margin; antepenultimate podomere devoid of setae; penultimate podomere with a single long seta arising from prominent notch on mid-extensor surface and with a short seta on apical end; ultimate podomere short and with three terminal setae.

Maxilla (Fig. 12) with unsegmented palp bearing two setae on apical end, the ventral one longer, heavier, and denticulate distally. Extensor surface of palp with prominent notch. Protopodite with two long, thin, terminal setae.

Copulatory Complex (Fig. 9). The proximal and distal portions of the base are not clearly distinguishable. Attached to the former are the short dorsal and long ventral fingers; the latter is more attenuate and is distinctly stalked subdistally. Both dorsal and ventral fingers terminate with the characteristic spine. The heavily sclerotized finger guard is conspicuously narrow and long, with the distal end prominently trilobed. The distal portion of the base is wide dorsally tapering to an acute point ventrally. The posteroventral margin is sclerotized with two small tooth-like projections at the ventral ex-

tremity. The horizontal and vertical rami of the clasping apparatus (Fig. 10) are not clearly delimited, and do not occupy the descriptive positions; for this reason they are here referred to as the proximal and distal rami. The former is approximately one-half as long as the latter and the angle formed by the two is about 60 degrees. The distal ramus is enlarged distally with six or more subapical serrations of which the two proximal ones are most prominent.

Female.—The valve of the *triunguis* forms (Fig. 13) is higher posteriorly than that of the male, and the ventral margin has a slight concavity just anterior to midlength. The dorsal margin is prominently arched, the anterior one smoothly rounded, and the posterodorsal margin concave. The measurements of ten specimens from the type locality mounted in Hoyer's solution exhibit a range in length of 0.465 to 0.510 mm, averaging 0.491 mm. The range in height is 0.300 mm to 0.330 mm, with an average of 0.312 mm.

The second antenna of the *triunguis* female has two or three terminal claws, of which the ventral one is thicker, longer, and heavier toothed. The unstalked dorsal claw is about three-fourths as long as the heavier ventral claw, and bears a few teeth on the distal end. The inconspicuous middle claw is without teeth and is two-thirds as long as dorsal claw.

The genitalia of the *triunguis* female (Fig. 13) are subtriangular and show considerable variation. Unlike other members of this group, the *triunguis* female is without the deeply staining mass associated with the genitalia.

No description can be made of the *biunguis* female as no copulating forms were observed.

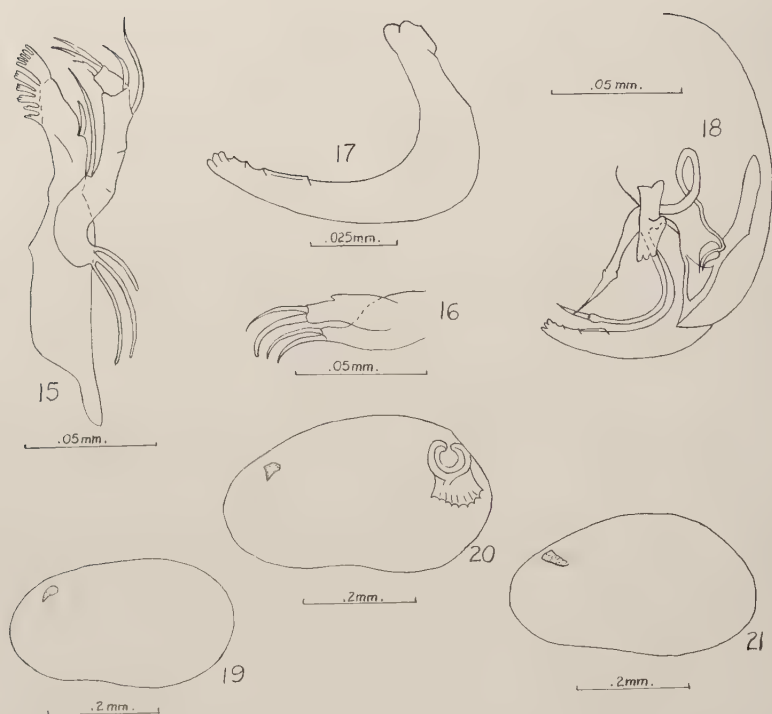
Type Locality.—East Fork of the Chattooga River at its junction with Indian Camp Creek on the grounds of the U.S. Fisheries Station, 21 miles northwest of Walhalla, Oconee County, South Carolina. The hosts are *Cambarus asperimanus* and *Cambarus bartoni bartoni*. Two other ostracods, *E. humesi* Hoff (1943) and an undescribed species were collected from the type locality.

Disposition of Types.—The holotype, the allotypic (*triunguis*) female, together with a dissected male paratype are deposited in the United States National Museum. Paratypes are in the collections of Drs. Horton H. Hobbs, Jr., Eugene N. Kozloff, and the author.

Range.—This species is known only from the type locality.

Variations.—There is remarkable uniformity in the male copulatory complex except that the finger guard is slightly wider in some specimens than in others. There are slight variations in the valve shape of both male and female.

Remarks.—*E. leptophylax*, without question, is to be placed in the Runki Group Crawford (1959) by virtue of the possession of the finger guard, an accessory process of the copulatory complex. The intragroup affinities of this species are highly uncertain as there appears to be a marked contrast between the copulatory complex of



Figs. 15-21.—*Entocythere chelomata* sp. nov. 15. Mandible of male. 16. Maxilla of male. 17. Clasping apparatus of male. 18. Copulatory complex of male. 19. Lateral aspect of valve of biunguis female. 20. Lateral aspect of valve of triunguis female. 21. Lateral aspect of valve of male.

E. leptophylax and those of the other four species of this group. The expanded apical end of the distal ramus of the clasping apparatus is similar to that of *E. humsi* Hoff (1943).

*Entocythere chelomata*⁴, sp. nov.

Male.—Valve (Fig. 21) oval in lateral aspect with margins smoothly rounded. Posterior end higher than anterior with maximum height just posterior to midlength. Prominent eye located one-fifth of valve length from anterior end. Setae sparsely distributed on lateral surface and dispersed as usual along free margin. Valve size is relatively constant as indicated by measurements of ten specimens from the type locality mounted in Hoyer's solution: length 0.420 mm to

⁴ Cheloma G. a notch; so named because of the notch on the finger guard of the clasping apparatus of the male.

0.465 mm, average 0.448 mm; height 0.250 mm to 0.270 mm, average 0.264 mm.

Antenna I similar to that of *E. leptophylax* described above.

Antenna II composed of four podomeres of which the basal one bears the antennal flagellum on apical end. Second podomere with feathered, spine-like seta borne on distal flexor margin. Penultimate podomere with two setae on apical flexor margin. Ultimate podomere divided distally with spine-like seta on midflexor margin of proximal portion, and bearing distally three terminal claws: dorsal one stalked with flattened, toothed distal surface; middle claw short with ten or more long teeth along ventral margin; and ventral claw longest and arched distally with a row of conspicuous teeth on ventrodistal surface.

Mandible (Fig. 15) with protopodite bearing six or seven multicuspid teeth; proximal two bicuspid, the next three tricuspid, and the distal tooth with five cusps. Heavy, spine-like seta borne on convex surface of protopodite proximal to proximal tooth. Respiratory plate with three setae, two subequal in length, and the third one half as long as the others. Palp consisting of four indistinct podomeres; except for the antepenultimate, each podomere with one or more setae.

Maxilla (Fig. 16) with protopodite bearing two long, thin setae distally and respiratory plate with about 20 plumose setae proximally. Unsegmented palp with two apical setae; the ventral one heaviest and apparently expanded distally. Convex surface of palp with slight notch opposite level of apical end of protopodite.

Copulatory Complex (Fig. 18). Attached to the indistinctly delimited proximal portion of the base are the short dorsal and long ventral fingers with spinous apices. The heavily sclerotized finger guard appears to be partially divided transversely at midlength, and the distal portion is broader than the proximal and trilobed apically. The posterior margin of the distal portion of the base is smoothly rounded terminating distally in an acute angle. The vertical ramus of the clasping apparatus (Fig. 17) is distinctly arched, is clavate proximally, and bears a prominence on the posterior margin. The longer horizontal ramus is slightly arched and bears four serrations on the distal half of the flexor margin and three prominent teeth on the apical end.

Female.—The valve (Fig. 20) of the triunguis forms is subovate with concavities on the posterodorsal and ventral margins, the latter being slightly anterior to midlength. The pubescence is similar to that on the valve of the male. The size is relatively constant as indicated by the measurement of 10 specimens from the type locality mounted in Hoyer's solution show a range in length of 0.435 mm to 0.480 mm, averaging 0.456 mm. The range in height is 0.255 mm to 0.300 mm, with an average of 0.278 mm.

The second antenna of the triunguis females has two or three

terminal claws, the ventral one being longer, heavier, and more prominently toothed than the smaller dorsal claw. The dorsal claw is three-fourths as long as ventral one and with few, if any, inconspicuous teeth. The untoothed middle claw, when present, is very narrow and about three-fourths as long as the dorsal claw.

The unique genitalia of the triunguis female (Fig. 20) consist of a pair of conspicuous circular, O-shaped, rod-like structures ventral to which is a prominent "pleated skirt."

The valve of the biunguis female (Fig. 19) is similar to that of the triunguis female except that it is smaller and is lacking the posterodorsal concavity.

Type Locality.—West Fork of the Little Pigeon River, one mile south of Gatlinburg, Sevier County, Tennessee, on U. S. Highway 441, in the Great Smoky Mountain National Park. The hosts are *Cambarus longulus longirostris*, *Cambarus bartoni bartoni* and *Orconectes juvenilis*. Three other ostracods, *E. humesi* Hoff (1943), *E. daphnioides* Hobbs (1955), and an undetermined member of the Cambaria Group, were collected from the type locality.

Disposition of Types.—The holotype, the allotypic (triunguis) female, and the morphotypic (biunguis) female along with a dissected male paratype are deposited in the United States National Museum. Paratypes are in the collections of Drs. Horton H. Hobbs, Jr., Eugene N. Kozloff, and the author.

Range.—Besides the type locality, this species is known to inhabit the Sugar Fork (Cullasaga) River northwest of Highlands, Macon County, and the Valley River at Andrews, Cherokee County, North Carolina. In the Sugar Fork River the host was *Cambarus bartoni bartoni* and in the Valley River the hosts were *Cambarus bartoni bartoni* and *Cambarus longulus longirostris*.

Variations.—Slight differences occur in the degree of concavities on the anteroventral and posterodorsal margins of the shell. The circular, O-shaped, rod-like bodies of the triunguis female genitalia were noted to assume a U-shaped appearance in some specimens, and were found to protrude beyond the posterodorsal margin of the valve in a considerable number of them.

Remarks.—The closest relatives of this species seem to be *E. runki* Hobbs (1955) and *E. suteri* Crawford (1959), differing from the former in the slenderness of the horizontal ramus of the clasping apparatus, and the more proximal serrations on the finger margin of *E. runki* are much more prominent and evenly spaced than are those of *E. chelomata*. The over-all outline of the clasping apparatus of *E. suteri* is similar to *E. chelomata*. The proximal end of the vertical ramus of the clasping apparatus of *E. suteri* appears to be evenly rounded while that of *E. chelomata* is conspicuously knobbed. One of the outstanding features of this species is the unique genitalia of the triunguis female. The finger guard of *E. chelomata*, which places it in the Runki Group Crawford (1959), bears a distinct notch at midlength while those of *E. runki* and *E. suteri* are entire.

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Notes and Discussion

Spore to Spore Culture on Agar of *Stemonitis fusca*

Alexopoulos (Am. J. Bot. 46:140-142. 1959) reported for the first time the cultivation on laboratory media of a member of the Stemonitales, *Stemonitis flavogenita*. He was later (Am. J. Bot. 47:37-43. 1960) able to carry through its life cycle another species at present included in the same order, *Echinostelium minutum*. With the exception of these two species, members of the order Stemonitales have not been cultured on laboratory media, to the writers' knowledge. This communication reports the cultivation of a third member of the Stemonitales, *Stemonitis fusca* Roth.

Spores from sporangia which had fruited on bark in a moist chamber in the laboratory were transferred to 1.5 per cent Difco corn meal agar plates on October 3, 1959. Small plasmodia had developed in most of the plates in seven days, and large veins with active streaming were present two weeks after inoculation. The cultures were maintained at room temperature in the dark and given water and dry cereals at intervals. By January 15, 1960 the plates contained abundant plasmodia. In an effort to induce fruiting, some of the plates were placed in direct sunlight for three hours and in daylight thereafter. Within three days they had fruited.

The organism has been kept continuously in culture since that time, and spores from the third generation grown on agar have now produced plasmodia. A study of the method of plasmodium formation, the fruiting process, and other phases of the life cycle is in progress.

The plasmodium of *Stemonitis fusca* corresponds closely with that of *S. flavogenita* as described by Alexopoulos. The plasmodium is delicate and almost transparent until fruiting is about to occur; at that time it becomes white and opaque. It has never been observed to turn yellow in our cultures. The long main veins with very short secondary branches are the outstanding characteristic of the well-developed plasmodium, in contrast to the fan of the Physarales. At the forwardmost portion of the moving or feeding plasmodium, however, anastomoses becomes more frequent, so that in this area the morphology of the physaraceous fan is approached. The high incidence of vacuoles as described for *Stemonitis flavogenita* was noted also in our material.

Our thanks to Professor G. W. Martin and Professor C. J. Alexopoulos for verifying our determination of the *Stemonitis* species.—SISTER M. ANNUNCIATA McMANUS and SISTER M. VIANNEY RICHMOND, Mount Mercy College, Cedar Rapids, Iowa.

Book Reviews

IN AND OUT OF THE IVORY TOWER. The Autobiography of Richard B. Goldschmidt. University of Washington Press, Seattle. xiii + 352 p., 27 figs. 1960. \$5.75.

Richard B. Goldschmidt died on April 24, 1958, just twelve days after his eightieth birthday and less than a week after completion of this manuscript. We are indebted to Dr. Curt Stern and to Dr. Leonie K. Piternick for the arduous task of seeing it through to publication.

This book is complementary to "Portraits from Memory," in which Goldschmidt presented his recollections of the great German zoologists of the late eighteenth and early nineteenth centuries. Many of the same people—Bütschli, Boveri, R. Hertwig, and so many others—appear in both books. In the Portraits, however, these men are the central figures, Goldschmidt only the narrator. The present book is his own story, and the others appear as his teachers, collaborators, and colleagues. All of these men met and worked together in the Ivory Tower of the academic community, but they took long excursions "out," and we see Goldschmidt not only as the man who developed the Kaiser Wilhelm Institute for Genetics, but also as a world traveller, an enthusiastic collector of art, a *bon vivant*, a mountain climber and hiker, and a devoted husband and father.

Because the emphasis is placed outside the Ivory Tower and because the glimpses within avoid technical aspects of his work, this book will be as comprehensible and fascinating to the educated public as to biologists. In the first chapters, there is given an insight into education in late imperial Germany which, to this reviewer, was as absorbing as it was informative.

Three times Goldschmidt visited Japan and other Oriental countries, and he also travelled widely elsewhere. The story of these travels is told with an excellent selection of interesting incidents and sympathetic and discerning description of the local cultures.

The tragedy of two World Wars looms large in this story. Goldschmidt was "caught" in the U.S. when World War I broke out. A patriotic German, he wanted to return and serve in the army. This was not possible, but he did succeed in bringing his family to the U.S. Although he had research facilities at Yale, he and his family were exposed to bitter enmity simply because they were Germans. After the U.S. entered the war, he was interned as an enemy alien. Even during this humiliation, he played the violin in a symphony orchestra, taught a course in biology in the camp "university," studied Spanish and Chinese, and wrote a book which was later very successful and was translated into several languages.

The disintegration of Germany after the war is graphically presented, as is its recovery, starting in 1924. But after a brief period of prosperity in what he described as the best equipped genetics laboratory in the world, the rise of the Nazis began. Although he remained at the Kaiser Wilhelm Institute until 1935, he saw what was coming, and began looking for a position abroad. When he was fired, he had already arranged for a lecture tour in the U.S. After some anxious months, he was called to the Berkeley campus of the University of California, which he describes as the "most congenial and charming of all universities on earth." Even here the shadow of Hitler fell, for he was again declared an enemy alien, and was subject to absurd restrictions until he became a U.S. citizen in 1942.

This is an intensely personal and frank narrative. Some readers will object that he sounds vain in some passages, particularly when evaluating his achievements. Those of us who knew and loved this great scholar knew that this is a misapprehension. He had a generous appreciation of the work of others which is not consistent with vanity. He has simply evaluated his contributions to biology honestly, without false modesty, as he would evaluate those of a colleague. The book concludes with a list of his publications. These number 248 in all, including 19 books, 133 papers on various aspects of genetics, 4 in protozoology, 27 in cytology, 8 in embryology, 11 in histology and neurology, 7 on cephalochordates, and many miscellaneous papers—enough material for several good careers! Surely, such a man has a right to a sense of satisfaction as he reviews his professional achievements!—EDWARD O. DODSON, University of Ottawa, Ottawa, Ontario.

QUAILS AND PARTRIDGES OF NORTH AMERICA: A BIBLIOGRAPHY. By Charles G. Crispens, Jr. University of Washington Press, Seattle, Washington. 1960. xii + 125 p. \$3.25.

Almost two thousand references from 72 journal sources appear in this non-annotated bibliography of 10 species of quails and partridges. Coverage is extensive enough to span all the way from *The Ibis* to the various state propaganda magazines. Foreign language literature has for the most part not been covered, and no attempt was made to include material from Pittman-Robertson Reports. For the chief species, Bobwhite, California Quail and Gray Partridge, the references are classified as follows: food habits and nutrition, life history, mortality factors, management, and reproduction.

This bibliography will be useful to students. It is not with ungratefulness therefore that the following weaknesses are observed. The basis for inclusion or exclusion of references is neither stated nor apparent; as a result one feels that that compilation has no objectivity. While the compiler noted the impossibility of attaining completeness, it is difficult to reconcile his stated hope that the book "will serve as a foundation to be built upon in subsequent years" with his failure to define what his collection represents and what it does not. Which journals were covered, how completely, between what dates, and for what type of literature? While nobody can blame a compiler for avoiding the difficult task of sifting through Pittman-Robertson Reports (though prepared by trained research biologists) it is incongruous that a compiler could use the time and effort thus saved to list articles from dozens of *Outdoors Regionalia* (written or rewritten largely by Madison Avenue penmen).

The author would have done well to omit several species altogether for they are covered only tokenworth. In fact a more exhaustive treatment of a single species would have been a far more useful contribution. The failure of a bibliographer to use American Ornithologists' Union Check-list nomenclature is inexcusable (both vernacular and scientific names are incorrect in this bibliography) even though many who write in the wildlife field are unfortunately unaware of this standard of usage. The author's use of "Coturnix Quail" in place of the more desirable "Common Coturnix" is consistent with his mixing *Alectoris* and *Perdix* with odontophorine quail. This reviewer deplores the publishing of a purely mechanical bibliography of this kind when there are perfected bibliographic media extant and when creative contributions to journals must be editorially rejected or emasculated in the name of economics. A bibliography of this kind seems an ill afforded luxury but I am glad to keep it as a luxury.—DAVID KENNETH WETHERBEE, Mass. Coop.

Wildlife Research Unit, U. S. Fish & Wildlife Service, University of Mass., Amherst, Mass.

DRAWINGS OF BRITISH PLANTS. Part XIV. Adoxaceae Caprifoliaceae. Rubiaceae. Valerianaceae Dipsacaceae. By Stella Ross-Craig. G. Bell & Sons, Ltd., London. 1960. 30 Plates. 10/6 (\$1.47).

This part presents *Adoxa moschatellina*, 8 species in 5 genera of Caprifoliaceae, 17 species in 4 genera of Rubiaceae, 8 species in 3 genera of Valerianaceae, and 5 species in 4 genera of Dipsacaceae, native to the British Isles. In each of the families of this part, there are species which are native, cultivated, adventive or naturalized in this country. Some of the noteworthy species are: *Sambucus nigra*, the large and showy European Elder; the delightful twin flower, *Linnaea borealis*; *Asperula odorata*, frequently used in the making of May Wine; the Garden-Heliotrope, *Valeriana officinalis*, and Fuller's Teasel, *Dipsacus fullonum*.

The usual level of high quality in representation of perspective views and magnified sections of all of the significant parts and growth characteristics of the species presented is maintained in this part.—L. G. KAVALJIAN, Sacramento State College, Sacramento.

METHODS OF VEGETATION STUDY. By Edwin Allen Phillips. Henry Holt and Co., New York. xvii + 107 p. 1959.

Methods of Vegetation Study is a field manual, done somewhat in the manner of a laboratory manual, apparently for use both by instructors and students. The plan which governs its content is stated on the first page of the Introduction, as follows: "The taxonomist in studying an area makes a list of species which constitute the *flora*. The ecologist begins with the floristic list and by a series of sample plots of observations ascertains the quantitative or qualitative relationships of the various species of the flora, leading to a concept of the *vegetation*. This book is concerned with various methods of sampling and with the treatment of data thus gathered." And further: "This book is in the field of synecology, or plant sociology." In explanation of the varied nature of the content of his book the author has this to say in the Preface: "At present there is a great diversity of concepts and methods in vegetation study. This diversity is proper and characteristic of a young, vigorous, developing field of science, but it produces confusion, particularly to the beginning student." And: "One approach to the teaching of elementary ecology most generally followed is the concentration upon one system to avoid this confusion. This book takes the other approach, the simplified presentation of several different systems from the European continent, Great Britain, and America."

The book contains 25 chapters divided among seven Parts. Fifty-six field exercises are described in the various chapters, from one to thirteen in each. At the end of the book is a list of the literature cited in the text and lists of selected books and journals that might be used in teaching with the manual. There is an Appendix containing lists of equipment and supplies needed for the exercises, and a general Index to the whole book.

Part One is on "Preliminary Survey" and contains a single chapter, on mapping. It is almost entirely on the use of a Bruton-type compass. With

another half-page the author could have described simple plane tabling (there is room for it on page 5), and the chapter would have been greatly improved. Part Two, also with a single chapter, is on "Physiognomic Systems—The Study of Vegetation on a Nonfloristic Basis." Here are field exercises to illustrate use of the life form system of Raunkiaer, the profile diagrams of the British ecologists, and the more recent systems of designation of form categories developed by Küchler and Dansereau. Part Three, on "Floristic Systems," has five chapters. Three of these, with appropriate exercises, are on the obvious questions of the roles of individual species in the total vegetation: "Frequency," "Abundance and Density," and "Cover and Basal Area." The other two chapters are on methods of sampling: "Transects," and "Plotless Methods." Part Four, on "Succession," contains three chapters: "Succession in Place," "Succession Study by Permanent Plots," and "Succession Studies by Surface Profiles and Transects."

Part Five, entitled "Analytic Qualitative Concepts," is a curious one. It is about two pages long and consists of one chapter called "Sociability, Vitality, Periodicity, and Stratification." Shorn of all its unnecessary verbiage and numbers (the authors of its methodologies appear unable to remain unquantitative), it seems to suggest that it might be worthwhile to walk through the vegetation and just look at it, for whatever might be there to see!

The longest section of the book is Part Six, on "The Synthesis of Data from Different Stands." No doubt it was also the most difficult for the author to write, for he had to thread his way through a maze of controversial issues. The thirteen chapter headings will suggest not only the content but also the difficulties involved: "The American Clementsian System," "A British System of Dominance by Scales of Estimate," "Presence," "The Continuum," "Vegetation Formulas," "The Degree of Maturity of a Plant Community," "Community Coefficients," "The Study of Communities on the Basis of Percentage, Density, Frequency, Basal Area, and Size Classes," "The Study of Forest Associations on the Basis of Percentage Canopy Composition in Long Transects," "The Study of Communities by the Use of Contiguous Quadrats," "Study of Communities by Correlation Coefficients," "Reduction of Sampling Error by Stratification of the Sample," "Synthesis of Data on the Basis of Scatter Diagrams." Part Seven, with a single chapter, is on "Artificial Populations."

The book will be useful for those who need a teaching schedule for elementary instruction in synecology, and for those who need a ready and simplified reference book on the complex of methodologies in use or proposed for the study of "vegetation." It is of handy size, easily carried around in a coat pocket. The illustrations, in the form of tables and text-figures, are adequate.—HUGH M. RAUP, Harvard Forest, Harvard University.

ORCHIDS IN AUSTRALIA. By Fred Moulen. Charles T. Branford Co., Boston, Massachusetts. 148 p. 1958. \$15.00.

This remarkable book is a photographic record of the beauty of a hundred orchids. The illustrations, reproduced from 35 mm Kodachromes, have captured the color of these prize-winning flowers. The title does not refer to orchids indigenous to Australia, but rather to those favored by Australian fanciers, such as species, varieties, and hybrids of *Cymbidium*, *Cattleya*, *Cypripedium*, *Vanda*, *Dendrobium*, *Miltonia*, and *Odontoglossum* among others. The text is restricted to a very general introduction and to brief legends indicating something of the history and growing conditions of the

flowers depicted. It is a book intended for those who revel in the colors and forms found in such profusion among the orchids.—G. T. A. BENDA, University of Notre Dame.

SOUTHERN FOREST SOILS. Edited by Paul Y. Burns. Louisiana State University Press, Baton Rouge 3, La. March, 1960. ix + 132 p. Illustrated. \$4.00.

With the advent of intensive forest management in southeastern United States, interest in forest soil productivity in this region has developed rapidly. As a consequence, the theme of the 8th Annual Forestry Symposium sponsored by the Forestry School at Louisiana State University, held in 1959, was southern forest soils. This book constitutes the proceedings of the 1959 symposium.

Topics considered by the 17 authors include the physiography of the southeastern United States, relationships between soils and tree physiology, various aspects of soil moisture and evapo-transpiration, a lengthy discussion of soil productivity estimates by means of site-index determinations, measures for improving productivity of forest soils including use of fertilizers, irrigation and drainage and a provocative inquiry into the biological potential of the southern forest region.

The papers concerned with these different aspects represent, for the most part, appraisals of the pertinent existing knowledge of soil-forest relationships. Throughout the book, the major emphasis is directed toward the use of this knowledge in obtaining maximum production of cellulose. It is not surprising that some of the measures suggested for achieving the desired goal are identical with those used in highly intensive forms of agriculture and horticulture. This approach constitutes a radical departure from the cut-out and get-out attitude that dominated the thinking of most foresters less than five decades ago. It will be very interesting to watch the future development of this field-crop philosophy in forestry.—G. K. VOIGT, School of Forestry, Yale University, New Haven, Connecticut.

THE BIOLOGIST'S HANDBOOK OF PRONUNCIATIONS. By Edmund C. Jaeger. Charles C. Thomas, Springfield, Illinois. xvi + 317 p. 1960. \$6.75.

"Terrific vocabulary but poor plot" could well characterize this listing of over 9,000 commonly used and frequently mispronounced terms in the biological sciences. The preferred pronunciation is given for each term with less frequently used but acceptable alternatives following. Although approximately 10 per cent of the terms listed are defined, it is regrettable that the remainder were not.

Obviously, the inclusion of any term in this listing is dependent upon the appraisal of the author. However, there seems to have been a rather arbitrary method of selection used, so that one searches in vain for such commonly mispronounced terms as gila, hirudin, abducens, luciferase, kyphosis and Acanthocephala. Duodenum is listed, but ileum and jejunum are not. One also finds systole but no diastole; homocercal but no heterocercal; Neognathae but neither Agnatha nor Gnatha; Chordate but no Protozoa; anabolism but no catabolism; carapace but no branchiostegite; amphipod and isopod but no crustacean; and Malphigia but no Cowper's. Hominidae is not listed nor is Onychophora, but per - ip' - a - tus is.

One misspelling was noted — speleology. The spelling given is not acceptable even as an alternative according to Webster's Unabridged International Dictionary.

For one not possessing an unabridged dictionary, this would serve as a convenient reference volume. It seems better adapted to the needs of botanists than zoologists.—BROTHER G. NICHOLAS, F.S.C., University of Notre Dame.

BEEKEEPING IN THE TROPICS. By Francis G. Smith. Longmans. London, 1960. xvii + 265 p. illustrated. \$11.25. (Obtainable from Longmans, Green, and Company, New York.)

There exist a multitude of books and bulletins on practical aspects of bee culture, published in many languages and in many parts of the world, and written with varying degrees of competence. At least to one who is not a beekeeper, most of them seem unnecessary, for they are very repetitious.

This book falls in a class of its own for it is the only book designed to be useful to beekeepers of the tropics. The author's experience is primarily in Africa but presumably most of his suggestions would be valuable in other tropical areas. Tropical Africa is blessed by the presence of one of the most vigorous and productive races of the honeybee, *Apis mellifera adansonii*; it seems likely that its introduction to other areas would prove a boon to tropical apiculture. An unusual feature of the book is the information provided on managing bees in small primitive hives. Concrete information on costs, expected profits, etc. under African conditions is included, together with rather detailed instructions on how best to do most of the things that a beekeeper must do.

The non-beekeeping biologist will find interesting the references to the many behavioral differences between various races of *Apis mellifera*. The book as a whole, however, is designed for practical use and is of little interest to the average biologist. Apiculturalists should, of course, have it on their shelves for reference even if they do not live in the tropics.—CHARLES D. MICHENER, The University of Kansas.

TAXONOMY OF FLOWERING PLANTS. By C. L. Porter. W. H. Freeman and Company, San Francisco and London. 452 p., 660 illustrations. 1959. \$6.75.

The author of this volume aimed to present a simplified account of the basic principles of taxonomy that would bridge the gap between texts that are really reference books for advanced students and meatless abbreviated treatments. In general he seems to have accomplished this, albeit in a stilted orthodox fashion. In attempting to find a middle ground between detailed presentation and meatlessness, there is always the possibility that too little information will be worse than none at all. This would appear to be the case in some instances in this book.

Part I, comprising the first 142 pages, deals with "the historical and theoretical aspects and with terminology and morphology." The historical account hits the usual highspots of pre-Linnean and Linnean periods, sketches landmarks of progress in the development of phylogenetic systems, and concludes with a brief and scarcely illuminating section on recent developments.

The chapters on taxonomic literature and nomenclature are separated by one on field and herbarium methods. Inasmuch as the last paragraph in the

literature chapter introduces the subject of the International Code, without indicating there that there is more to follow elsewhere, the nomenclature chapter might logically have followed immediately.

In Chapter 6, "Concepts of Taxa," Professor Porter seems to achieve his middleground in regard to the concepts of genera and higher categories. However, his treatment of the species concept, admittedly a difficult one to handle, would seem to be at once too much or too little. Certainly the beginning student of taxonomy will be ill-equipped after such a brief discussion to cope with the concept of the species based on experiment and presented in tabular form taken from Clausen, Keck, and Hiesey.

There is a short chapter on the construction and use of keys which is a highly desirable feature of a taxonomy text. The value of key construction as a teaching and learning device has been under-emphasized. The comparatively great advantages of an indented key over a bracketed key, except to editors and printers (who do not count), is not sufficiently emphasized. The chapter on keys, whereby necessary morphological terminology is used, would be more effective, if it had followed rather than preceded, the chapter on phytophraphy and terminology.

The latter chapter is, with exception noted below, nicely done, well illustrated, and supplemented at the end of the book by a suitable glossary. It includes an exposition on the construction and use of floral diagrams in which the author has worked out some nice refinements.

An instance of what often proves to be a terminological snarl to students is with us again in this book. In the chapter on terminology we find that "Pistils, collectively called the gynoecium, are the female reproductive parts of the flower and occupy a central position. The gynoecium may consist of a single pistil, as in the Lily, of several or many pistils, as in the Buttercup." And that "The basic unit of construction of a pistil is the carpel. . . ." "A pistil may consist of a single carpel, . . . or of two or more carpels partly or completely joined together, . . ." "One can usually determine the number of carpels in a pistil by sectioning the ovary and counting the number of partitions. . . ." "When a pistil is composed of a single megasporophyll, or *carpel*, it is termed a *simple pistil*. When it is composed of two or more carpels that are more or less united, it is a *compound pistil*." It is interesting to note that the basic unit of structure of the pistil is the carpel and that a pistil may consist of a single carpel. By this token is the unit of structure of a pistil also a pistil?

Appropos of these terms we find the following phrases in the keys and in the descriptions of the orders and families later in the book:

gynoecium usually of 3 carpels, which are distinct; the pistil 1, of 1 or more carpels; the pistil 1, of 1 carpel; carpels 2; carpels 3, united; pistil 1, of 2 united carpels; carpels 1-many, separate or united; pistils simple; pistil 1; carpels free; carpels 1 or more; carpels (pistils) usually numerous; pistil of 2-5 carpels; gynoecium of separate carpels; carpels usually 2; carpels usually few; carpels 2-5, often 3.

The example "carpels usually 2;" comes from the description of an order. Each family in that order has "pistil 1, of 2 united carpels." The example, "carpels usually few," comes from the description of an order. The families within that order have "pistil 1, usually of united carpels," and "pistil 1, of 2-5 united carpels." The instructor, if he is old enough, has become inured to this and takes it in stride. The student, if he is kind, smiles sweetly and with the barest suggestion of a shake of the head seems to say, "I have to pass this course. Who am *I* to question?"

Universally nowadays, morphologists consider the carpel the unit of struc-

ture of the gynoecium. A gynoecium may be comprised of a single carpel, two or more separate carpels, or two or more carpels fused in which case it is said to be syncarpous. Pistil appears to be a term that got there first historically. It also appears to have become superfluous but here tradition gets the upper hand. It is scant comfort to a student, whose mind is not initially saddled with a feeling for the sacredness of tradition, to have to wrestle with terminology which has outlived its usefulness, or which is a cause of befuddlement, simply because it has been with us a long long time.

With regard to the concepts of, "simple pistil," and "compound pistil," one might logically (Heaven forbid), consider a sepal as a simple calyx, a gamopetalous calyx as a compound calyx. Similarly, a petal might be considered a simple corolla, a gamopetalous corolla a compound corolla.

This reviewer was pleased to find Professor Porter was not reluctant to let serve the terms hypogynous, perigynous, and epigynous whose derivations are such that their meanings are easily understood, therefore readily taught. This pleasure was, however, soon mixed with some chagrin, for the author's amplification relative to the use of the terms led to an unnecessarily complex analysis for beginners. If each of the three terms has some reasonable separate identity, I am at a loss to reconcile simplicity with the following "Six Basic Morphological Flower Types": 1) the hypogynous flower; 2) The perigynous flower with free hypogynous hypanthium; 3) The perigynous flower with the floral axis expanded continuously; 4) The perigynous flower with adnate hypogynous hypanthium; 5) The epigynous flower without a hypanthium; and 6) The epigynous flower with an epigynous hypanthium.

My criticism of the categories elaborated above is not meant to be construed as favoring the continued wide use of the old "superior" and "inferior" whose omission from the chapter is praised — *even though regrettably they frequently creep in incognito, as it were, in keys and in diagnoses of orders and families later in the book*. Neither does the author consistently, nor even usually, adopt for his own use in keys and diagnoses the six basic flower types outlined above. A cursory tally was made of this with the following results: hypogynous was used alone sixty times; perigynous was used alone fifteen times; epigynous was used alone twenty-nine times; basic type 2 was used once; basic type 4 twice; basic type 5 twice; basic type 6 thrice; some alternative combination of wording of the basic types eight times.

According to the author's own definitions, either directly stated or by inference, the terms perfect and unisexual refer to *flowers*; the terms monoecious, dioecious, polygamous, polygamo-monoecious and polygamo-dioecious refer to *plants*. This is correct. It appears, however, that wherever the author has occasion to use one of the series of terms referring to *plants*, he uses it as applying to *flowers*. For example we find "flowers monoecious or dioecious," "flowers monoecious, dioecious, or polygamous." "flowers polygamous." This is incorrect usage. Certain other authors (some of widely used books) are guilty of precisely this same incorrect usage. Precedent for inaccuracy by no means justifies its perpetuation.

Chapter 9, entitled, "Angiosperms" is devoted to the classification of the group, the criteria used, and some proposed schemes of classification. The question arises why certain of the features of Chapter 2, "Historical Summary," are presented there and not integrated with Chapter 9, or vice versa. The discussions on classification and classification systems in the two chapters referred to seems to be either too little or too much — too little for clarification to the student of the sense of any putative phylogeny; too much not to make the student confused about it all. If there be any reasonably acceptable phylogenetic scheme which has worth in teaching beginning students, let it be

shorn of the vicissitudes of its historical development as interwoven with the historical development of other such schemes. Present it for whatever value it has in getting beginners to think in these terms. Surely it is not necessary to indicate in so doing that this is the only or the last word. Moreover, if it is worthwhile to pursue and ponder phylogeny at all, then it behooves an author of a textbook to present orders and families in whatever phylogenetic sequence he feels has most merit.

The classification of the monocotyledons adopted by the author in "Part II, Selected Orders and Families of Monocotyledons," includes three subclasses which are briefly explained in the chapter on Angiosperms, namely, Calyciferae, Corolliferae, and Glumiflorae. The Calyciferae and Corolliferae are reputedly distinguished by the biseriate perianth of the former, the sepals and petals unlike in texture and color; the perianth of the latter is uniseriate and often petaloid throughout. The Corolliferae includes the Liliales as its basic order, and amongst others the Amaryllidales, the Iridales, the Arceales, and the Orchidales. The author's floral diagrams for *Lilium*, *Narcissus*, *Iris*, *Synechanthus*, and *Orchis*, representatives of the above orders respectively, all clearly show biseriate perianths!

A feature associated with the presentation of representative orders and families which at first seems to offer help for classwork and obviating, one hopes, the necessity for a separate complimentary set of keys, is a simple key for each principal group, *i.e.*, for the Calyciferae, the Corolliflorae, etc. However, having got through the monocotyledons and past the Floriferae in the dicotyledons, the help is at an abrupt end. There are no keys to the orders and/or families of the large Polypetalae and Sympetalae (although there are some keys within orders of these). A set of separate, supplementary keys is necessary after all.

The utilization of space on the pages upon which appear the precise terminological diagnoses of the orders and families is such as to leave plenty of space for the author to have described with *some* feeling, at least, characteristics of living plants representing these categories. As it is, and as is usually the case, the impoverished delineations scarcely permit the thought that Nature ever breathed any life and glory into her creatures. Botanists are said to have imparted an odor to botany. If it is a continuing process, possibly they might yet gild the lily with some fragrance.

During the last several years much has been said by prominent persons in august society meetings and written by them in profound journals about revitalizing the teaching of biology, especially botany. Much of this has emanated from academic or near-academic maestros or near-professional pontificators. A few good healthy swipes have been taken by interested "outsiders." Even smaller fry and run-of-the-mill practitioners occasionally back off to give a few moments thought to whether or not it has anything to do with them.

Just two years ago at this writing, a panel of distinguished systematic botanists published a "Suggested Outline for Teaching Systematic Botany" wherein attention was called to their instructions, *viz.*, "'the objective is not to replace one orthodoxy by another but rather to stimulate continuing re-evaluation and experimentation in teaching practice,'" and to "'throw the subject out the window' and start over." In gathering information on outlines of courses being taught around the country the panel could but consider that they (the courses) had as a common denominator, "pious platitudes."

One may perhaps be forgiven for asking whether this is just read into the record. Revitalized teaching, to be sure, begins in the classroom. But unless teachers abandon the practice of having their students use textbooks, a very necessary part of the revitalization must become part and parcel of textbook

writing. A student, as often as not, will come to his first meeting of class with textbook in hand. Not infrequently he will have had interest (or curiosity) enough to have taken a gander at its contents. If it be a textbook in taxonomy, I fear he will have formed a prejudice such that the teacher will have to give it all he has got to revitalize *the student*, for the text is about as likely to have sent bubbles up the nose as a bottle of champagne opened in the days of Theophrastus—who like as not greeted him on page 1.—ROBERT K. GODFREY, Florida State University, Tallahassee.

BEEKEEPING. By John E. Eckert and Frank R. Shaw. Macmillan Co., New York. 536 p., 150 figs. \$12.50.

This textbook of apiculture is a much needed revision of E. F. Phillips' "Beekeeping" (Macmillan, 1915). The original has been the standard text in apicultural courses for many years, and it is good to have it brought up to date. There have been many advances during the past 45 years, not only in the applied field of apiculture, but also in our basic knowledge of honey bee biology and behavior. Eckert and Shaw, apiculturists at the University of California and at the University of Massachusetts, have done a commendable job of integrating much of this new information in their revised edition. It should remain the standard text for years to come. I believe that the next edition, if one is contemplated, should contain a section on human sensitivity to bee venom and the problems of desensitization; medical men are likely to look for some discussion of this problem in a book on the honey bee.—KARL V. KROMBEIN, Entomology Research Division, U. S. Department of Agriculture, Washington, D. C.

BIRD PORTRAITS IN COLOR. Text by Thomas S. Roberts, M.D., Revised by Walter J. Breckenridge, Dwain W. Warner, and Robert W. Dickerman. University of Minnesota Press, Minneapolis. 92 pls. 1960. \$5.95.

Illustrations of two hundred and ninety-five species, first produced for "The Birds of Minnesota" are again available with a revised text. The plates are well known for the inclusion of sexual, ontogenetic and seasonal variation in plumage. They represent the work of Walter J. Breckenridge, Allan Brooks, Louis Agassiz Fuertes, Francis Lee Jaques, George Miksch Sutton and Walter Alois Weber.

The text material facing each full page plate begins with a brief characterization of each family. For the various species remarks on the distribution and, especially where pertinent, notes on habitat, food, nesting, song and behavior are included. The chief revision of the text has been in matters of distribution and taxonomy, an updating to conform to the last edition of the A. O. U. Checklist. An index contains both scientific and official vernacular names, as well as certain appropriate local or popular names.

Although originally produced for Minnesota ornithologists, the illustrations include a major representation of the avifauna of the Mississippi Valley; thus the book will be useful to naturalists in eastern North America.—ROBERT E. GORDON, University of Notre Dame, Notre Dame, Indiana.

Theodor Karl Just
1904-1960



Theodor Karl Just, 1904-1960

When Theodor Karl Just died on 14 June 1960 at his home in Oak Park, Illinois, the world of science, and of men, was deprived of a unique person. It was the end of a life of a scientist, and of a man, who devoted more time to the work of others, and to them, than he did to his own work, or to himself.

He was born in Gross Gerungs, Austria, on 27 October 1904. His mother was Anna Traindl. His father, Alois, whose avocation was the ecology of the region, was a teacher who became superintendent of the school system of Krems, Austria, 40 miles west of Vienna. Judged by its products, the household was a scholarly, cultured one, for there were three sons—one a physician, one a Ph.D. in music, and one, the botanist Ted Just, who, in everything and to everyone, demonstrated gentility, an appreciation of the arts, sincere interest in other persons, and continuous devotion to selfless scholarship.

His boyhood interest in natural science, fostered by his father's own interest in it, developed into a career in botany. He obtained the Ph.D. at the University in Vienna in 1928. For the year following, he was an assistant in the herbarium at the Museum of Natural History in Vienna.

In his last year at the University in Vienna, he became the friend of Rev. F. J. Wenninger, C.S.C., who was studying there. Father Wenninger, head of the Department of Biology and Dean of the College of Science at the University of Notre Dame, was one of the important people in Dr. Just's life. He persuaded Dr. Just to join the faculty of Notre Dame. In 1929 he came as Instructor in Biology and Curator of Botanical Libraries and Herbaria. He remained at Notre Dame for seventeen years. During these years, he matured as a scientist, editor, and administrator, and formed lasting associations with the University. He was instructor from 1929 to 1933, Assistant Professor to 1936, Associate Professor to 1941, Professor to 1945, and J. A. Nieuwland Research Professor in Botany from 1945 to 1946, when he resigned to go to the Chicago Natural History Museum. At the Museum he was Chief Curator of the Department of Botany from 1947 until shortly before his death.

At the death of Father Wenninger in 1940, he was appointed head of the department, and held this post during the difficult years of the war. He brought the best of the European scientific tradition to his job as department head. He visualized a department representing both experimental and non-experimental Biology (*i.e.*, no emphasis on one at the sacrifice of the other). In this atmosphere he believed that a student could develop a broad outlook and gain a general appreciation of Biology and its relation to other scientific disciplines under the guidance of a staff who were contributing to knowledge in their fields of interest. Because of the unusual teaching demands caused

by the war, balanced progress was not easy. And, finally, the enormous amounts of time required by his other activities forced him to choose in favor of the Chicago Natural History Museum, where he could devote time to his other interests. In the five years as head of the department, he made a lasting impact, and a solid contribution to the University. During this time, despite the difficulties of maintaining and building a staff, he saw the department become a lively teaching and research center. While at the Museum in Chicago he continued his university associations as Research Associate in the Department of Biological Sciences at Northwestern University, and as Professorial Lecturer in the Department of Botany at the University of Chicago. From 1938 he was also Scientific Director of the Lloyd Library of Botany, Pharmacy, and Materia Medica in Cincinnati, Ohio.

One of his outstanding characteristics was his interest in scientific accomplishment itself, and the pride he could take in the role of others in it. So it is appropriate, and perhaps a required consequence, that probably his greatest permanent influence was effected through his activities as an editor. Upon his arrival at Notre Dame, he made a second important friendship — that with Father J. A. Nieuwland, the chemist and botanist. Father Nieuwland persuaded Dr. Just to be assistant editor of *The American Midland Naturalist*, a small journal devoted to the natural history of the region, and he was its editor from 1935 until 1946. With his friend, Prof. J. H. Hoskins of the University of Cincinnati, he founded the journal *Lloydia* in 1938 and was its first editor.

Through the pages of *Lloydia* in his score of years as Editor have come a variety of articles each attesting to his successful efforts to implement the flow of scientific information.

From 1940 he was an assistant editor of *Chronica Botanica*. He also edited such publications as "Plant and Animal Communities" in 1939, and a series of monographs from 1944 to 1946.

The monographs appeared as Nos. 1, 2 and 3 in *The American Midland Naturalist Monograph* series. The establishment of this series during the period of the Second World War was fraught with problems other than those usually thought of as editorial. A perusal of the correspondence attendant to the publication of the first monograph reveals his optimism when confronted with paper shortages and delay due to lack of printing facilities and personnel. In founding this series, he provided one of the few outlets in this country for publishing longer manuscripts.

His roles in founding *Lloydia* and *The American Midland Naturalist Monographs* are clear. Not so obvious is his contribution to the development of *The American Midland Naturalist*. He set out to broaden its scope, both in content and in geographical influence, and he succeeded. At the beginning of his editorship he made it almost a one-man task, functioning as editor and publisher, spending many hours at his editorial desk or in the printshop. His editorial function sometimes included reworking manuscripts almost to the point of complete rewriting. In this way he was directly, but anonymously, respon-

sible for the production of excellent scientific papers that, without his work, would have been something less, or perhaps would not have existed. He believed it his duty to become personally and intimately involved as much as necessary to produce the best possible paper if the material offered was good, and it probably never occurred to him to reject a paper containing substantial observations and ideas just because it was badly prepared, and would mean countless hours of work for him. In performing these duties, he was living his beliefs that he described when he wrote that editors "must function as public servants creating the all-important liaison between contributor and reader through the medium of their journal . . ." and that "they work for the benefit of the maximum number of people and the advancement of science." It is apparent that he considered his editorships as an important life purpose, and that he fulfilled this purpose zealously. He insisted that his friend Father Nieuwland be given prominent credit for founding *The American Midland Naturalist*; we can insist that Dr. Just be given credit for making it an important scientific journal.

His chief contributions to botany and paleobotany stemmed from his ability to synthesize literature, to prepare up-to-date reviews or summaries, and to prepare publications and promote research. His articles were skilfully written and generally "covered the field" with careful balance. Such articles as "Progress in Paleobotany, 1908-1958," "Fossil Floras of the Southern Hemisphere and their Phytogeographical Significance," "Gymnosperms and the Origin of the Angiosperms," "The Rates of Evolutionary Processes," "Pharmacopoeias, Dispensatories, Formularies and Allied Publications," and "Geology and Plant Distribution," indicate his wide interests and breadth of comprehension. These and similar writings, though each is usually but a few pages long, are comprehensive syntheses of the literature.

In botany, Dr. Just's writings were concerned largely with summarizing the history of ideas, resolving confusion in terminology, taxonomy and morphology, encouraging and summarizing ecologic studies and his study of certain members of the Chenopodiaceae. A most important botanical contribution was his encouragement of many professional botanists and students to write up their ideas, to engage in certain types of research, to study certain problems, and to translate important foreign works. To many of these works or writings, he made direct contributions, usually known only to the author or researcher whom he was encouraging. This influence often took the form of precise advice, suggestions, bibliography, translations, re-writing of manuscripts, suggesting names, clarifying rules of taxonomy and nomenclature, obtaining funds or publication media, or introducing botanists to one another. He was responsible for helping numerous botanists find a locale or institution receptive to their work, and for bringing a number of people together for collaborative studies.

Paleobotany was a challenging field of interest which gave Dr. Just a satisfying diversion from his editorial routine and his botanical reading and writing. His fundamental concern for paleobotany developed in his long association with Professor Hoskins of the Univer-

sity of Cincinnati. Hoskins, a student of Chamberlain at Chicago, was keenly interested in plant morphology. It was a similar interest in Dr. Just's repertoire that afforded the plane on which their lifelong friendship first developed. "Doc" and "J.H.," as they always called each other, made a point of getting together two or three times a year. They took a number of field trips together during their earlier years. Typical of these were botanical trips to bogs and swamps of Indiana and Michigan, and forays to such botanically unique or interesting spots as "Tight Holler" or Natural Bridge, Kentucky.

Their paleobotanical trips were numerous, including one memorable trip, in the summer of 1941, to many of the principal fossil plant localities in western United States. There, in company with Aureal T. Cross and Arthur H. Blickle, they visited Iowa coal-ball localities; climbed to the "Mecca" of American paleobotanists, the gigantic fossil *Sequoia* stump high up on the side of Specimen Ridge in Yellowstone Park; tramped the arid country of the John Day beds in Oregon; searched for *Tempskya* along pioneer overland trails in southwestern Wyoming; "scratched" for cycads below the crest of the Dakota and Lakota hogbacks above the "racetrack" in the Black Hills area; probed for petrified *Ginkgo* wood in the lava flows of the Columbia River in Washington; and hammered on the mid-Devonian channel fill at Beartooth Butte for *Psilophyton*.

Dr. Just was not physically powerful, but he was enthusiastic and persevering in the rough field work, and he thoroughly enjoyed the accompanying camping routine. On these excursions he constantly "taught" his companions the latest in morphology, often from some of the most obscure foreign publications, or discoursed at length on taxonomic and nomenclatorial matters to the extent that one student was heard to remark, "This trip sounds like a plenary session of the Roman Senate!"

Dr. Just made important contributions to general paleobotanical literature and American paleobotany. He developed several review papers which were exceptionally scholarly in organization and valuable for broad coverage. He was in the forefront of the work of the Paleobotanical Section of the Botanical Society of America, serving several years as secretary and later as chairman. He also represented that organization on the Editorial Board of the *American Journal of Botany* and brought together three extensive summaries of activity and bibliographies of paleobotanical work in the country, the last of which, for the years 1952-1957, was published in *Lloydia* after his death.

He had become quite interested in the Mesozoic flora during the last ten years of his life and studied the broader aspects of the morphology and evolution of the cycads and their relationship, along with other gymnosperms, to the primitive angiosperm stocks. He designed and supervised the construction of some very remarkable exhibits of cycadeoid plants at the Chicago Natural History Museum.

One of Dr. Just's most remarkable characteristics was his extensive knowledge of biological literature, both in books and journals. He was a proficient linguist and seemed to delight in scanning books and articles in any of several languages and then give his friends lucid

summaries of these at late night coffee meetings or afternoon "tea-breaks." His more than 150 published "Reviews," most of them of extensive treatises or books, represented only a small portion of those he read and then discussed with his colleagues. The authors of many manuscripts which were submitted to him for publication in *The American Midland Naturalist* or in *Lloydia*, learned of the tremendous scope of his knowledge of the literature when they received his suggestions concerning their bibliographies.

On the national and international level, he discharged many society and committee duties. At times, he was Vice-President and President of the Indiana Academy of Science, Secretary to the Paleobotanical Section of the Botanical Society of America, Chairman of the Committee on Paleobotanical Nomenclature of the same section, Secretary and Vice-President of the Society for the Study of Evolution, Chairman of the Committee on Paleobotany of the National Research Council, Chairman of the Committee on Editorial Policy of the Conference of Biological Editors, and Vice-President of the Conference. The last activity was a significant one to him in the last part of his life. During the war he was consultant to the Office of Strategic Services.

As most of us, Dr. Just had many cares. Especially important to him were the welfare of his mother and his two brothers (one killed in an air raid) during the war; the deaths of his friends Father Nieuwland, Father Wenninger, Dr. Lyon, and Professor Hoskins; the unfortunate misunderstandings arising from certain administrative decisions that always were honorably motivated; his grief for his young family as he lived out his last months with certain knowledge of his imminent death. Unlike most of us, however, he kept his cares to himself. Only a few — and perhaps only one — of his friends appreciated his burdens. To most people, Dr. Just was friendly, warm, affable, smiling, able and helpful, a botanist and editor that we sought out, for he helped us with our difficulties and never troubled us with his. One who was privileged to talk with him on the brink of his death saw Ted Just as he always had been, talking of *Lloydia*, manuscripts, science (he furnished a reference), children, and of how we must get together soon for an evening of Hugo Wolf and Schubert — with flute, piano and voice, as we did many years ago.

What were the important things in his life? Professionally — his broad interest in biology, his sincere, unselfish concern for biologists and their development and progress, his frank admiration of scholarship, his association with the University of Notre Dame, and, most important, perhaps giving him more satisfaction and sense of accomplishment than any other, the "Midland" which is his memorial. Personally — his numerous friends and the warm relationships he had with them, and his temporal source of solace and strength, his wife and three daughters. His home was the center of his life. One saw the best of a good man there. *Requiescat in pace.*—A. T. CROSS and E. L. POWERS.

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* We are indebted to Dorothy Gibson and Lillian A. Ross of the Chicago Natural History Museum for their kind assistance in the preparation of this bibliography—EDITOR.

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The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 65

APRIL, 1961

No. 2

A Study of Homing in the Cotton Mouse, *Peromyscus gossypinus*

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ABSTRACT: Homing success of animals released in unnatural habitat (golf course) adjacent to their home area was less than in natural areas at comparable distances. In natural areas, males homed with greater success than females from distances greater than 500 feet. In unnatural areas there was no sex difference. Initial orientation in unfamiliar territory could not be correlated with the direct route home. The distance of the homesite from the release area (1000 feet to 60 miles) apparently did not influence initial orientation. Repetitive liberations of successfully homing mice from the same release site on the golf course indicated that mice can learn homing pathways. Mice which had homed a number of times and were then held in captivity for periods of more than 12 weeks before being liberated at former release sites showed no decline in their homing ability. Animals released in their former home ranges occupied prior to extended periods of laboratory isolation remained and maintained these areas. Animals without previous experience from artificial displacement returned to and maintained their former home ranges when released at various distances from their capture sites after prolonged laboratory isolation. The results indicate that cotton mice are capable of learning and retaining for prolonged periods of time a schema of their environment and are able to utilize this information in homing activity.

It is postulated that psychological factors are the principal source of motivation to home. Based on the degree of psychological attachment to an area small rodents may have three types of zones: 1) Territory; 2) Home range; and 3) Life range. The latter is considered to be all the area an animal traverses during its lifetime.

The present data are interpreted to indicate that the mechanism of homing in *P. gossypinus* involves random movements outside the life range with respect to the homesite and directed movements in relation to the home area from within the life range. In the latter case the animal utilizes a previous familiarity (mnemotaxis) with the general area gained by occasional exploratory wandering, home range shifting, and dispersal from the birthplace. Each of these movements apparently involves environmental imprinting.

INTRODUCTION

Homing ability and the general problem of spatial orientation have received increasing attention in recent years and have been investigated in widely diverse groups of animals. A considerable number of studies of small terrestrial mammals, principally rodents, have included information on the homing ability of the species con-

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cerned (*e.g.*, Aldous, 1937; Allen, 1938; Andersen, 1951; Bowers, 1954; Burt, 1940; Butsch, 1954; Feniuk and Demiashev, 1936; Feniuk and Popova, 1940; Feniuk and Sheikina, 1938; Hacker and Pearson, 1951; Hamilton, 1937, 1959; Harrison, 1958; Hungerford and Wilder, 1941; Johnson, 1926; Kalabukhov and Racoskii, 1933; Keith and Waring, 1956; Kendeigh, 1944; Layne, 1954, 1957; Linsdale, 1946; Löhr, 1938; McCabe, 1947; Murie and Murie, 1931, 1932; Rawson, 1956; Schleidt, 1951; Schmid, 1936; Seton, 1909; Stickel, 1949; Townsend, 1935). Data on homing have been obtained more or less incidentally to other aspects of the biology of the species being studied. Relatively few investigations, such as those of Rawson (1956), Schleidt (1951), and Stickel (1949), have dealt specifically with homing behavior of small mammals and have involved systematic field and laboratory procedures.

The information presently available on homing in small mammals clearly indicates that there is a general tendency among individuals of many species to return to their home areas when artificially displaced.

There are two major aspects involved in seeking to understand homing behavior in small mammals and other animals as well. The first of these concerns the nature of the motivation to return home. In other words, why should an animal placed in new surroundings similar to those in its home area exhibit a strong inclination to return to its previous quarters? This consideration leads to the question of what factors in the environment of a small mammal constitute "home" to that animal and what is the underlying psychological and physiological basis for the recognition of, and attachment for, the home area. Although much attention has been given to measurements of home range size in mammals, the problems of the psychological implications of the home range to the individual have thus far been largely neglected.

The second aspect involves the actual means utilized by an animal in its efforts to return to the home area. Various hypotheses concerning this problem have been suggested. Some workers such as Chitty (1937) and Layne (1957) have proposed that animals return from unfamiliar territory through random wandering until and if familiar surroundings are encountered, whereas others, including Burt (1940), Feniuk and Popova (1940), Feniuk and Sheikina (1938), Neuhaus (1948), and Vogelburg and Kruger (1951), have postulated the existence of some special sense of direction. The possibility that some animals actually possess a greater range of familiarity with the area around their homes than conventional study techniques indicate has also been suggested as a factor in homing success (Chitty, 1937; Kendeigh, 1944; Murie and Murie, 1931; Stickel, 1949, 1954).

The present paper concerns an investigation of homing behavior in the cotton mouse, *Peromyscus gossypinus* (LeConte), in north central Florida. The study, utilizing approximately 175 individual

cotton mice, involved: 1) establishment of home range and population estimates as necessary background for other phases; 2) displacements at various distances from the capture site to determine the extent of homing ability in natural areas; 3) homing releases in unfamiliar and unnatural habitat of animals from adjacent natural populations at distances similar to those used in natural areas for the purpose of comparing homing performance, 4) observations on initial orientation with respect to the homesite of animals released in unfamiliar and unnatural habitats, and 5) retention experiments involving the holding of animals in laboratory isolation for extended periods of time to learn the effects of such treatment on subsequent homing performance and home range recognition.

Acknowledgments.—I wish to express my appreciation to Dr. James N. Layne for his helpful criticism and numerous suggestions throughout the course of the investigation. Drs. Pierce Brodkorb, Robert DeWitt, Lawrence Hetrick and James Redmond read the manuscript and helped in various ways. I am indebted to Mrs. Helen Phifer Glass for her generosity in permitting the use of her property at San Felasco for ecological studies. Dr. H. K. Wallace and Messrs. William H. Etheridge, Dale Birkenholz, Lee Frazer, Glenn Simpson and J. Hill Hamon assisted me during some phases of the study. Financial assistance was received from the Florida Academy of Sciences, and field work during the summer of 1957 was made possible by a fellowship from the College of Arts and Sciences, University of Florida. This paper is part of a doctoral dissertation submitted to the faculty of the graduate school of the University of Florida.

DESCRIPTION OF THE STUDY AREAS

The studies were conducted at four localities in Alachua County; these will be designated as San Felasco, Devil's Millhopper, Ft. Clark and the golf course.

The San Felasco area was located approximately 9 miles northwest of Gainesville. The general region consisted of an extensive mixed hardwood forest, with such trees as laurel oak (*Quercus laurifolia*), magnolia (*Magnolia grandiflora*), holly (*Ilex opaca*), sweet gum (*Liquidambar styraciflua*), and ironwood (*Ostrya virginiana*) being characteristic. This vegetative association, termed mesophytic hammock (Laessle, 1942), has been considered to represent the climax community of much of northern Florida (Figs. 1 and 2).

The Devil's Millhopper study site, located approximately 6 miles northwest of Gainesville, consisted of some 90 acres of mixed woodland with a network of trails and footpaths extending throughout the plot. The general aspect of the vegetation was similar to the San Felasco area except for some dry sections supporting grassy pine flatwoods. The Devil's Millhopper station was bordered on the south by a paved road and pine flatwoods and on the remaining sides by farmland.

The Ft. Clark area was situated about 8 miles west of Gainesville, and consisted of approximately 200 acres of mesophytic ham-

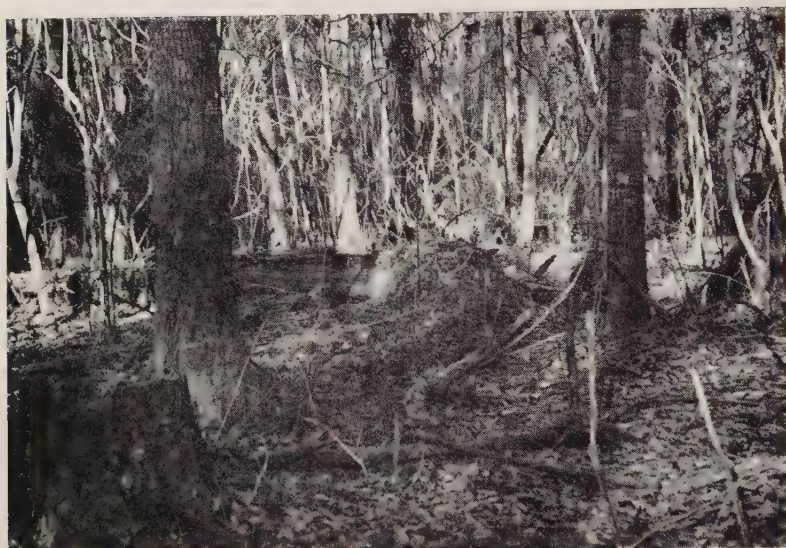


Fig. 1.—View of San Felasco study area.

mock that was somewhat drier than the San Felasco study site. The woodland was bisected by a sand road 50 to 65 feet in width. The area was generally flat and vegetatively relatively uniform throughout. It was bordered by farms, a limestone quarry, and the remnants of a cut-over pine flatwoods.

The golf course used in the study was located at the western edge of Gainesville. Its over-all dimensions were approximately 2200 by 2200 feet, and it was bordered on the north by a paved highway, on the east by a residential section, and on the south by cultivated lands of the University of Florida Agricultural Experiment Station. At the western edge of the golf course was a fringe of woodland bordered by a sand road. A hammock of approximately 40 to 45 acres in extent was situated on the other side of the road. The latter was 30 to 45 feet wide and was subject to frequent traffic during the morning and afternoon but little at night. The fairways of the golf course varied from 100 to 200 feet in width and were kept closely cut during the time the experiments were conducted (Fig. 3). The fairways were separated by park-like stands of oaks and pines. Although gray squirrels (*Sciurus carolinensis*) inhabited these stands, there was no evidence that cotton mice occurred there naturally.

HOME RANGE SIZE AND POPULATION DENSITY

In order to better interpret homing results, background information on the extent of normal movements of individual mice and on population densities in the habitat-types studied was obtained.

HOME RANGE

Data on home range were obtained at the San Felasco station. An area of approximately 20 acres was gridded with stakes at 100-foot intervals, giving a total of 88 trapping stations. Two types of live traps, the small (2 inches $\times$ 2 1/2 inches $\times$ 6 inches) Sherman trap and a plywood trap with inside dimensions of 2 1/2 inches $\times$ 3 inches $\times$ 8 inches, were used in this and other phases of the study. Rolled oats were used exclusively as bait. Trapping specifically for home range data was conducted for 11 nights during two periods, 6 nights from March 22 to March 28, and 5 nights from April 4 to April 9, 1959. Additional home range data for this population were accumulated incidental to other phases of the study until July, 1959.

All stations were trapped simultaneously with one trap per station. Mice were identified by a system of toe-clipping. Information recorded at each capture included date, trap station, sex and reproductive status, and escape path and refuge site used when liberated. Traps making captures were rebaited and reset at the same station but not in the same position as before.

Forty-eight cotton mice (25 males, 20 females, 3 juveniles) were trapped a total of 194 times during the course of the home range study. Four to ten captures were available for each of 25 adults (12 males, 13 females) taken a total of 145 times. Of the remaining 23 animals taken, 12 (1 adult male, 4 subadult males, 1 subadult female, 3 adult females, 3 juveniles) were captured only one time



Fig. 2.—General view of type of natural habitat in which studies were conducted.



Fig. 3.—View of one of the release points on the golf course.

each and 11 (4 subadult males, 4 adult males, 2 subadult females, 1 adult female) were taken two to three times each for a total of 26 captures.

Home ranges were calculated by the inclusive boundary strip method (Stickel, 1954) for the 12 adult males and 13 adult females taken a minimum of four times each.

The mean trap-revealed home range was $1.57 \pm .17$ acres. This value is comparable to that, $1.87 \pm .22$ acres, found by McCarley (1959) for *P. gossypinus* in Texas. The home ranges of 12 males averaged $1.82 \pm .36$ acres, with extremes of 0.45 and 4.36 acres, while those of 13 females averaged $1.44 \pm .19$ acres, with extremes of 0.22 and 2.75 acres. Although the difference in home range size between the sexes is not statistically significant, it suggests that males tend to have a larger home range than females. Other studies of this species indicate a similar trend.

Pournelle (1950) reported wandering of up to 2800 feet for a male cotton mouse while females appeared to move much shorter distances, and Pearson (1953) found that females of *P. gossypinus* generally moved less than 125 feet between release and recapture while males generally moved more than 125 feet. Barrington (1949) has shown that males of this species sometimes wander more than one mile while females wander about 800 feet between captures. Larger average home range size for males than females has been found for other species of *Peromyscus* (Burt, 1940; Blair, 1940, 1942) and similar data are available for a variety of other small mammals.

POPULATION DENSITIES

The number of mice estimated to be resident on the San Felasco study area was 36 (20 males, 16 females), which is equivalent to 1.6 animals per acre. Only mice with two or more captures were considered as residents, and the density is calculated on the basis of an adjusted sampling area which compensates for the probability of some animals having home ranges extending beyond peripheral traps (Dice, 1952). A rough estimate from live trapping results indicated that population densities were relatively the same at the four study sites.

HOMING IN NATURAL HABITATS

Mice used in homing experiments were removed from the traps in the morning and maintained in the laboratory until the time of liberation at night, thus eliminating at least some of the supposed effects, such as increased predation, of releasing nocturnal animals during the day. The mice were always conveyed to and from the study area and laboratory in numbered traps placed in a large container. The movements involved in transporting them over the study area and in the car are considered to have prevented the animals from utilizing kinesthetic cues in subsequent homing tests. Great care was taken to reset traps in the same place each time in an attempt to increase the probability of recapturing an animal upon its return.

Homing experiments were carried out at three natural study areas. Since the methods of study differed somewhat in each of these, the results of the experiments in each area are treated separately below.

SAN FELASCO

Following completion of home range studies, homing experiments were conducted on the trapping grid at this station. Individuals were displaced at relatively short distances beyond the limits of their known home ranges. A displacement of 300 feet was approximately equal to the diameter of the average home range. Animals were recorded as having successfully homed if they were recovered at any station within their calculated home range. Eighteen mice were trapped and displaced during an 18-day interval of irregular trapping. All trap stations were activated during each trapping period. Animals returning from their first release were often released in another direction and at a different distance. Thus, 5 mice were liberated one time, 6 mice were liberated two times, 1 mouse was liberated three times, 4 mice were liberated four times and 2 mice were released five times.

Initial releases were made as follows: 2 males and 1 female at 100 feet, 1 male and 1 female at 150 feet; 1 male and 2 females at 200 feet, 1 male and 1 female at 300 feet, 1 female at 400 feet, 2 females at 500 feet, 2 females at 600 feet, 1 male at 800 feet, and 1 male and 1 female at 900 feet.

Of the 7 males and 11 females displaced, all of the males and

10 of the females successfully homed. A male released at 300 feet was recovered on one occasion one-half the distance to its home range before it was recaptured in its home area. The female that was not recovered was an adult released at 600 feet.

Subsequent liberations of successfully homing animals included 19 releases of females as follows: 2 at 100 feet, 1 at 150 feet, 1 at 200 feet, 2 at 250 feet, 3 at 300 feet, 1 at 350 feet, 2 at 400 feet, 2 at 500 feet, 1 at 550 feet, 2 at 600 feet, 1 at 750 feet, and 1 at 800 feet. In a series of 9 males, 2 were released at 200 feet, 1 at 250 feet, 2 at 300 feet, 1 at 500 feet, 2 at 600 feet, and 1 at 700 feet. Recoveries were made in the case of all males and 18 of the 19 female releases. The female not retaken had been released a second time at a distance of 500 feet in the opposite direction from the first liberation at 600 feet.

The trapping schedule used at San Felasco was such that traps were not always available until several nights following releases. Therefore, it is not possible to present a detailed analysis of the times required for homing at this station.

It is of interest to note that although in many cases released mice had to travel through a portion of the grid of traps to reach

TABLE I.—Results of initial releases in the three natural habitats

Distance displaced	Animals displaced		Animals recovered	
	Males	Females	Males	Females
Feet				
100	2	1	2	1
150	1	1	1	1
200	1	2	1	2
300	1	1	1	1
400	..	1	..	1
500	4	6	4	6
600	..	2	..	1
800	1	1	1	1
900	2	1	2	1
950	1	1	1	1
1000	2	2	1	2
1050	3	..	2	..
1150	1	..	1	..
1500	2	2	2	1
2000	2	3	2	1
2100	..	1	..	1
2500	4	2	2	0
Totals	27	27	23	21

their respective home ranges, only one individual was taken in a trap beyond the boundaries of its previously calculated home region.

DEVIL'S MILLHOPPER

Homing experiments in this area were conducted using 30 trapping stations spaced 20 paces apart in an L-shaped trap line. Two traps were set at each station. Single displacements of 8 males and 9 females were made at distances ranging from 500 to 2000 feet from the place of capture. The releases were made during a trapping period of six consecutive nights in March, 1959, and traps were available for recapture on the night of liberation. Mice were considered to have successfully homed if they were retaken at the original site of capture or in either of the adjacent stations. The 17 displacements included in Table I were made as follows: 2 males and 2 females at 500 feet, 2 males and 2 females at 1000 feet, 2 males and 2 females at 1500 feet, and 2 males and 3 females at 2000 feet. Of these mice, 7 males and 6 females homed.

FT. CLARK

At this study area, homing tests were performed with 12 males and 7 females during April, May, and June, 1959. Two trapping periods were used, each of six consecutive nights. Ten trapping stations were established. Five were located on each side of the sand road about 50 feet within the woodland at intervals of approximately 100 feet. Three traps, spaced 10 to 15 feet apart, were used at each station. Release distances ranged from 400 to 2500 feet from the site of original capture, and mice were considered to have homed only if they returned to any of the three traps at the station of original capture. Successfully homing mice were liberated a number of times, usually at another distance and a different direction from that of their first release.

TABLE II.—Animals that were unsuccessful in homing from initial releases at Ft. Clark and Devil's Millhopper

Release distance	Sexes and numbers of animals		Number of consecutive nights traps were available following release
	Males	Females	
Feet			
1000	1	--	4
1050	1	--	5
1500	--	1	4
2000	--	2	5
2500	1	--	3
2500	--	1	4
2500	1	1	5

Ten mice were liberated 1 time, 2 mice were liberated two times, 4 mice were liberated three times, 2 mice were displaced four times, and 1 mouse was released five times. The numbers, sexes and distances involved in the initial releases of the 19 animals are included in Table I. Thus, 2 males and 2 females were released at 500 feet, 1 female at 800 feet, 1 male at 900 feet, 1 male and 1 female at 950 feet, 3 males at 1050 feet, 1 male at 1150 feet, 1 female at 2100 feet, 4 males and 2 females at 2500 feet.

Nine males and 5 females were recovered at the station where first captured, even though many of the displacements were made at a point that made it likely that the mice would encounter traps at several stations if they were to use the direct route in returning to their homesites.

Six of the 19 mice were displaced in the woodland on the opposite side of the road from which they were captured and 3 of these animals were recovered. Two of these individuals, a male and a female, had been displaced at 950 feet and the third, a male, had been released at 2500 feet. Those mice not retaken after removal to the opposite side of the road included 2 females liberated at 2500 feet and 1 male released at 1050 feet.

Of 20 subsequent releases, 9 of them were made in the woodland on the opposite side of the road from which they were captured. Five males released at 550, 850, 900, 1200 and 1450 feet, were retaken at their homesites and therefore had to traverse the sand road in returning. The 4 mice not retaken included a male and 3 females liberated at 1200, 500, 800, and 900 feet respectively. Apparently the road did not constitute a strong barrier to homing.

SUMMARY OF EXPERIMENTS IN NATURAL HABITAT

Of 54 mice (27 males, 27 females) displaced for the first time at distances ranging from 100 to 2500 feet, 44 animals (81%) were considered to have homed. Eighty-five per cent (23) of the males and 78 per cent (21) of the females returned. Every individual of both sexes homed from distances up to 500 feet. At distances from 600 to 2500 feet, 14 of 18 males (78%) and 9 of 15 females (60%) were retaken, indicating that males are more successful than females in homing from the greater distances (Tables I and II). A grand total of 101 releases (51 for males, 50 for females), including initial and repeated releases of homing animals, was made at distances varying from 100 to 2500 feet and homing was recorded for 83 per cent of the releases. Eighty-six per cent of male releases and 80 per cent of the female releases resulted in homing. Of the releases ranging from 100 to 500 feet, all of the males (17) and 92 per cent of the females (25 of 27) returned. Of the releases ranging from 550 to 2500 feet (34 male releases, 23 female releases) 79 per cent (27) of those of males and 65 per cent (15) of those of females returned home. At the Ft. Clark area 4 of 19 (21%) mice used in initial releases and 10 of 20 (50%) used in subsequent releases were recap-

TABLE III.—Results of subsequent releases of animals that successfully homed from initial releases at Ft. Clark

First release			Subsequent releases	
Sex	Distance in feet	Recapture interval*	Distance in feet	Recapture interval*
M	500 W	1	450 NE 1200 E	1 No recapture (3)**
F	500 E	2	400 N 900 SE	1 No recapture (3)**
M	500 W	2	450 NE 1200 SE	1 3
F	500 W	2	1150 E 2000 E	(3) (7) (46)*** 2
F	800 W	3	800 E	No recapture (2)**
M	900 E	2	1450 SE 2000 E 2500 E	1 1 No recapture (2)**
F	950 NW	1	500 N	No recapture (4)**
M	950 N	2	850 E 900 NE 700 W	1 1 1
M	1050 E	3	-----	--
M	1050 E	5	-----	--
M	1050 E	1	550 SW 850 NE 1200 N 1850 E	(1) (2) (41)*** 1 1 No recapture (3)**
F	2100 E	1	-----	--
M	2500 E	2	-----	--
M	2500 E	3	-----	--

* Night of release is designated as night 1.

** Figure in parenthesis indicates the number of consecutive nights traps were available immediately following release (uninterrupted).

*** First figure in parenthesis represents the number of consecutive nights that traps were available immediately following release (uninterrupted); second figure represents actual trap night the animal was recovered; third figure in parenthesis indicates the total nights elapsed between release and recapture.

tured on the night of liberation (Table III). This suggests, therefore, that homing performance of animals liberated away from home subsequent to the first successful homing trip tends to improve, even though the distances and directions of successive releases are varied.

The results of the homing experiments in natural habitats indicate that homing success in the cotton mouse is inversely proportional to distance at which released. There is a further indication that males and females home with equal success at shorter distances (<500 feet), while males have a greater probability of homing than females as release distances are increased. The data further suggest, although the relationship is not clear-cut, that, for the range of distances utilized, homing from the initial release is more rapid at the shorter distances (Table IV). Homing success also appears to improve at both short and long distances with repetitive liberations, even though these are not made at previous release points (Table III).

Similar results have been obtained in other studies. For example, Murie and Murie (1931) recorded 87.4 per cent return from displacements up to 900 feet and only 30.6 per cent from 1050 to 3900 feet for *P. maniculatus*, if only those animals released away from home

TABLE IV.—Release/recapture intervals of initial releases at the Devil's Millhopper and Ft. Clark study sites

Release distance in feet	Animals recaptured in their home areas		Recapture interval in nights*
	Males	Females	
500	2	2	1
500	2	2	2
800	--	1	3
900	1	--	2
950	--	1	1
950	1	--	2
1000	1	1	1
1000	1	1	3
1050	1	--	3
1050	1	--	4
1150	1	--	1
1500	1	--	2
1500	1	1	3
2000	1	--	2
2000	1	--	3
2000	--	1	5
2100	--	1	1
2500	1	--	2
2500	1	--	3

* Night of release is designated as night 1.

for the first time are considered. Harrison (1956) working with *Rattus*, reported 83 per cent recovery from 1650 feet and 38 per cent recovery from rats liberated at 2640 feet. Hacker and Pearson (1951) have noted a similar trend in homing ability in *Apodemus sylvaticus*, and Burt (1940) in a study of *P. leucopus*, showed that 76 per cent of the mice were retaken from displacements of 30 to 465 feet while only 33.3 per cent of those liberated from 480 to 1095 feet were recovered.

HOMING FROM UNNATURAL HABITAT

From March to early September, 1959, homing studies were carried on at the golf course, utilizing mice from adjacent natural habitats. The object of this phase of the study was to obtain data on homing success from what could be considered totally unfamiliar and unnatural habitat for comparison with those obtained in natural habitats. Trapping was conducted in two wooded plots located in the northwest and southwest corners of the golf course and in the hammock west of the sand road. Sixteen trapping stations were established in the northwest corner where the habitat suitable for cotton mice was limited to approximately one-half acre. At the southwest corner 12 trapping stations were used, the area being somewhat smaller than that in the northwest corner. The same stations were used throughout the study. No particular arrangement or spacing of traps was utilized, and mice were considered to have successfully homed if retaken at any of the traps in which they were originally captured, since the areas were small enough to correspond with the home range of the animals. In the large woodland, 40 stations were arranged in a U-shaped pattern with about 30 yards between stations. Mice were recorded as successfully homing if retaken at the original site of capture or in either of the adjacent trapping stations. Single traps were used at the stations in the study plots at the edge of the golf course and two traps set within 10 to 20 feet of each other were used in the hammock west of the road.

Animals captured in the peripheral areas were released at selected sites on the fairways. No release site had trees nearer than 100 feet. Some of the successfully homing animals were released a number of times from the same release point to learn the effect of repetitive liberations in unnatural habitats on homing performance. In a very few instances, the release site was shifted between successive releases.

Forty-seven mice were initially released on the golf course at distances ranging from 1000 to 2700 feet from the site of capture in the adjacent woodlands. In all cases, traps were available for recapture for three nights, including the night of release, and in many instances for as long as 7 to 21 nights after each series of releases. Three males, 2 females, and 1 juvenile were released at 1000 feet, 1 male and 1 female at 1700 feet, 1 male and 2 females at 1800 feet, 4 males and 1 female at 1900 feet, 3 males and 3 females at 2200

feet, and 18 males and 7 females at 2700 feet. Fifteen of these animals (10 males, 5 females) were subsequently recovered at their homesites. All of the animals that returned from 1900 feet or more had to cross the sand road in order to reach their home areas.

One male that homed from 2700 feet was not recovered during the four consecutive nights that traps were available following displacement, but was recaptured on the third night after liberation at a point 2500 feet north of its original capture site. This individual was later recovered in its home area on the first night of a trapping period, 40 nights after the original displacement. Traps had been available to this animal a total of 14 nights between the time of liberation and subsequent recapture in its home area.

Several animals were recaptured at places other than their home areas. Two males and a female at 2700 feet and a male released at 2200 feet northeast of their respective homesites were trapped approximately 2500 feet north of the homesite. The single juvenile released 1000 feet west of its home area was recaptured 2200 feet south of the site of original capture, and a female displaced 2200 feet northeast of its homesite was recovered 400 feet east of the original capture site.

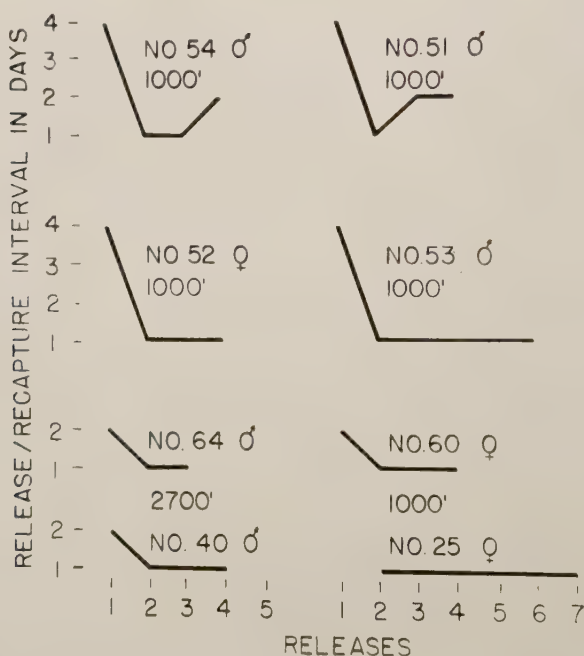


Fig. 4.—Effect of multiple releases from the same point on time of return in golf course experiments.

Seven of the 15 animals recaptured in the home area were liberated a number of times from the same release point. The results of these tests clearly indicate that the animals home more rapidly from the same release site following the first return. This trend is illustrated in Fig. 4, where the length of time taken by the mice to return from successive releases from the same point over distances of 1000 to 2700 feet is shown graphically. In most instances time intervals were measured in nights, since traps were checked only on the morning following release. However, on one occasion periodic checks were made after release and a close approximation to the actual time taken to return from 1000 feet was obtained for 3 animals that had homed from the same point previously. A female, No. 60, released for the third time, returned in less than three hours. Another female, No. 52, and a male, No. 53, which had been released for the third and fifth times, respectively, were back in the traps within two hours.

These results are summarized in Table V. Of 6 mice (3 males, 2 females, 1 juvenile) released at 1000 feet, only the juvenile did not return to its homesite. Ten mice (6 males, 4 females) were liberated at 1700 to 1900 feet and 3 males and 2 females were recaptured. Four males and 1 female, of 31 animals (21 males, 10 females) liberated at 2700 feet, were recovered. No recaptures were recorded on the night of release. Six of the 15 animals that homed returned by the second night following liberation; the other 9 mice took an excessive amount of time for recovery (Tables VI and VII). Of the total number of adult mice released (46) on the golf course at 1000 to 2700 feet, 5 of 16 females (31%) and 10 of 30 males (33%) returned to their home areas. Successfully homing animals released repetitively from the same point at distances ranging from 1000 to 2700 feet from the homesite clearly improved their homing performance.

TABLE V.—Results of initial releases in unnatural habitat (golf course)

Distance displaced	Animals displaced		Animals recovered	
	Males	Females	Males	Females
Feet				
1000*	3	2	3	2
1700	1	1	1	1
1800	1	2	1	1
1900	4	1	1	0
2200	3	3	0	0
2700	18	7	4	1
Totals	30	16	10	5

* One juvenile was displaced 1000 feet but was never retaken at its home area.

The data from homing releases made on the golf course provide a basis for comparison with those in natural areas. It should be pointed out that the highway, residential areas, and cultivated lands at the northern, eastern, and southern borders of the golf course could have acted as barriers to the animals and may have directed their movements to some extent. The sand road bordering the west side of the golf course may to some extent have been a barrier to homing but the recovery of some individuals from the mesophytic woodland on the other side of the road indicates that it probably did not hamper movements excessively. The results of the Ft. Clark experiment further support this contention.

The shortest distance at which releases were made on the golf course was 1000 feet. The homing success at this distance was closely similar to that in natural habitats. However, nearly all animals released at this distance in natural habitats were recovered by the second night following liberation. In the case of the golf course releases only 1 animal returned by the second night of trapping. Other animals released at 1000 feet took more than four nights to return.

Three of the 10 mice liberated at 1700 to 1900 feet on the golf

TABLE VI.—Release/recapture intervals of initial releases on the golf course

Release distance in feet	Animals Recaptured at their home areas		Recapture interval in trap nights*		
	Males	Females			
1000	--	1		2	
1000**	3	--	(4)	(5)	(35)
1000**	--	1	(4)	(5)	(37)
1700	1	1		2	
1800	1	--	(7)	(11)	(17)
1800	--	1		2	
1900	1	--		4	
2700	2	--		2	
2700**	1	--	(6)	(7)	(26)
2700**	1	--	(4)	(14)	(40)
2700**	--	1	(6)	(13)	(40)

* Night of release is designated as night 1.

** Figures in parentheses represent the following: First figure — the number of consecutive nights that traps were available for recapture immediately following release though the animal was not recovered during this time; Second figure — the actual trap night that the animal was retaken; Third figure — indicates the interval of time between release and eventual recapture.

course returned by the second night following release. All of these mice were residents of the southwest corner of the golf course which was near rows of pig pens on the Agricultural Experiment Station lands. The loud and frequent clanging of the feeding trough doors by the pigs may have provided an auditory cue for these mice which might explain their relatively rapid return. Two other mice homing from 1800 and 1900 feet took an excessive amount of time to be recaptured. Four of the 6 mice released at 2000 and 2100 feet in natural areas were retaken, 1 on the night of liberation, 1 on the second night, 1 on the third night, and 1 on the fifth night of trapping. In comparing homing success in natural habitat to homing success from the golf course, no clear-cut difference was found at release distances ranging from 1700 to 2100 feet although there is a tendency for mice to return more rapidly in natural areas.

Of the 31 animals released at 2200 feet or more on the golf course, only 2 were recaptured by the second night following release. Three other mice released at this distance took considerably longer, and as noted 1 of these was retaken 2500 feet north of its home-site before it was recaptured in its home area. In natural areas 2 of 6 mice released at 2500 feet were recaptured, 1 by the second and the other by the third night following liberation. Both of these were males. Considering that traps were available for recapture in

TABLE VII.—Animals that were unsuccessful in homing from initial releases on the golf course

Distance released	Males	Females	Number of nights that traps were available for recapture following release	
			Consecutive nights beginning with the night of release	Total nights
1000	Juvenile		7	14
1800	--	1	7	11
1900	1	--	7	18
1900	1	1	8	19
1900	1	--	10	21
2200	--	1	5	16
2200	2	--	7	11
2200	1	2	8	16
2700	5	1	3	3
2700	--	1	3	11
2700	--	1	4	12
2700	2	--	4	7
2700	5	3	6	14
2700	2	--	4	12

the peripheral areas of the golf course for a much longer period of time than in natural areas and that the nature of the area surrounding the golf course might have to some extent directed the movements of the animals westward, which was in the direction of the home area, the results strongly suggest that mice home with greater success in natural areas.

INITIAL ORIENTATION

From February to early September, 1959, observations were made on the initial movements of animals liberated at night on the golf course. Two groups of mice were used, a "local" series (also used for homing experiments) captured less than one mile from the release site and a "distant" series captured from four to 60 miles from the release area. The mice used in these experiments were captured in the morning and kept for 12 to 15 hours in the laboratory until the time of liberation at night. Several mice from the local sample were held in captivity up to 65 hours before release because of inclement weather, and 4 mice from 60 miles away were kept in the laboratory 13 days before release.

A step-ladder painted black for camouflage was used at the release site as an observation point. The experimental animal was transferred from a live trap to a bottomless hardware cloth cage measuring 5 inches $\times$ 3 inches $\times$ 3 inches and placed on the ground beneath the center of the ladder. After the mouse had been allowed a period of time for adjustment to its surroundings, the observer, seated on top of the ladder, gently raised the cage by means of an attached string.

A strip of cellophane tape with a 1 1/2 inch patch of luminous paint ("Lite Koat Mixture" manufactured by the General Cement Company, Rockford, Illinois) previously charged by a flashlight in a light-tight box was affixed to the dorsum of the mouse just before it was transferred to the release cage. After liberation the mouse was observed directly or with the aid of a pair of 7 $\times$ 50 binoculars. The pattern of its movements was traced in as great detail as possible on data sheets which also included the date, time of night, location of homesite, temperature, wind direction and velocity, sky conditions, and other details. The animals were marked for permanent identification by toe-clipping.

The maximum distance any mouse was observed from the release point was approximately 175 feet and many of the mice required 12 to 13 minutes to move beyond the observer's range of vision.

Overcast or moonless nights provided best conditions for observations. The luminescent patch remained visible for approximately 15 minutes. The initial movements of mice in both groups were characteristically slow and usually very erratic. Randomly selected examples of initial movements from the two groups are shown in Figures 5 and 6. In some instances the animals moved in spurts and occasion-

ally followed a more or less circular pattern, sometimes returning to the release point several times. No correlation between speed of departure or the animal's initial course and the proximity or direction of the homesite was apparent under a variety of environmental conditions, including overcast and clear nights with and without a moon. However, clear moonlit nights tended to inhibit movements of the mice, which seemed hesitant to leave the area of shadow created by the observation post.

Further evidence that initial orientation movements on the first release were random with respect to the homesite is provided by an analysis of the selection of particular directional zones by mice when released. An imaginary line was drawn from the release point to the approximate homesite. Using the home bearing at the base line, the release area was divided into four equal zones. Zone +I included the sector encompassed by a 45 degree angle on either side of the

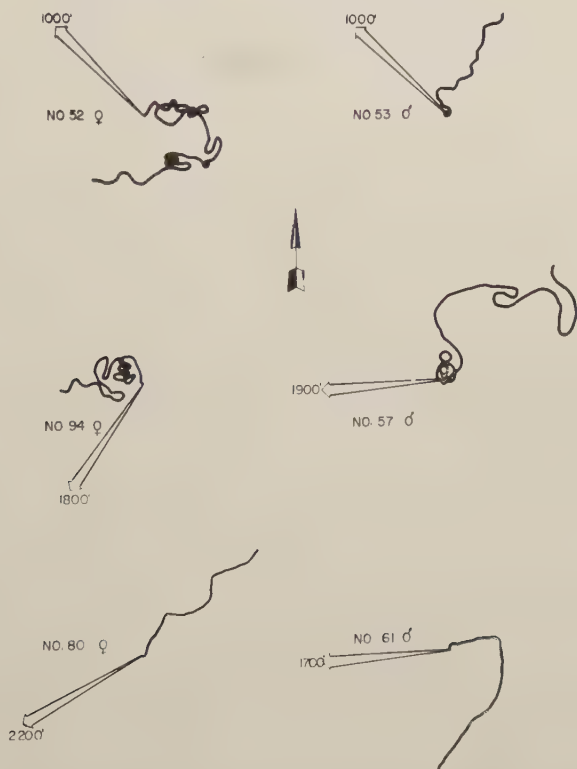


Fig. 5.—Initial orientation patterns in unfamiliar territory of mice from the "local" population. The direct homing route for each animal is indicated by the arrow originating at the release point.

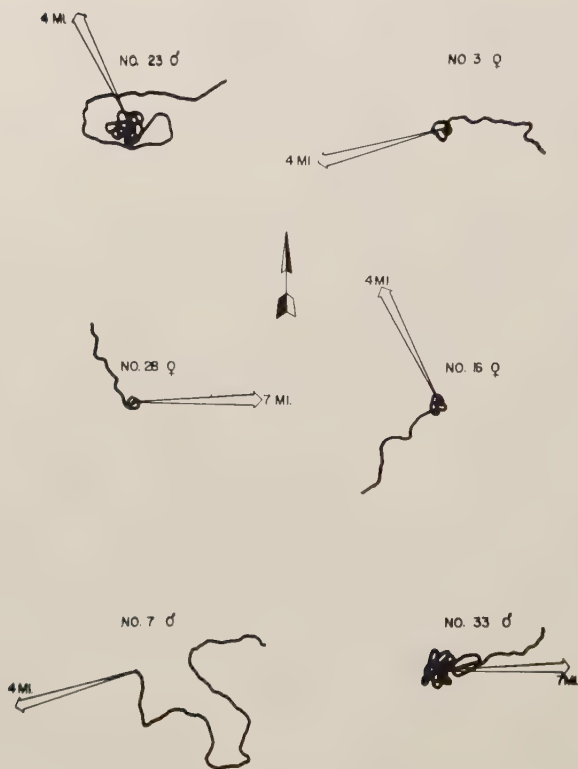


Fig. 6.—Initial orientation patterns in unfamiliar territory of mice from the "distant" populations. The direct homing route for each animal is indicated by the arrow originating at the release point.

home bearing. Zone -I included the opposite 90 degree sector, and the lateral zones were designated as 0_1 and 0_2 .

Of 47 mice comprising the local sample, 10 (6 males, 4 females) selected Zone +I, 11 (8 males, 2 females, 1 juvenile) Zone 0_1 , 12 (8 males, 4 females) Zone 0_2 , and 14 (8 males, 6 females) Zone -I. In the case of the 42 mice constituting the distant sample, 9 (6 males, 3 females) selected Zone +I, 11 (7 males, 4 females) Zone 0_1 , 8 (4 males, 4 females) Zone 0_2 , and 14 (6 males, 8 females) Zone -I. The difference in these frequencies are not significant in either series on the basis of the chi-square test (local sample $X^2 = 0.95$, distant sample $X^2 = 1.98$).

The 15 animals from the local population that were subsequently recovered at their homesites had selected the following zones on their first release: Zone +I, 1 male released at 1800 feet and a female released at 1700 feet; Zone 0_1 , 1 male released at 1000 feet, 1 fe-

male released at 1800 feet and a male and female released at 2700 feet; Zone O_2 , a male released at 1700 feet, 3 males released at 2700 feet and 2 females released at 1000 feet; and Zone -I, a male released at 1900 feet and 2 males released at 1000 feet. There is no significant difference in the frequency of use of the four zones by these animals, indicating that even in the case of successfully homing mice there was no tendency to select the direction of the homesite when released for the first time in unfamiliar territory.

Seven of the 15 animals were regularly liberated and recaptured a number of times from the same release point. The observed movements at later releases were strikingly different from those of the first. In almost every test, the mouse moved rapidly and with little hesitation, often passing beyond observation range within 30 seconds. During the course of these repetitive releases, it was noted that some

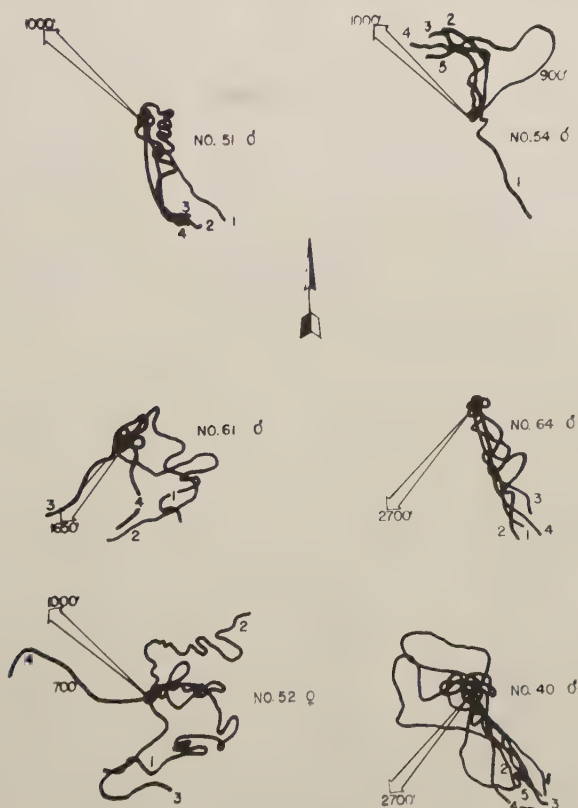


Fig. 7.—Initial orientation of 6 mice released repetitively at the same point on the golf course. The direct homing route for each animal is indicated by the arrow originating at the release point.

mice appeared to utilize the same initial pattern of movement as on the first release, even though the pathway was unoriented with respect to the home direction. Such a tendency is indicated by mouse No. 51 whose initial orientation patterns are shown in Figure 7. One animal, male No. 54, on its fifth release at a point 100 feet closer to the homesite than the usual distance (1000 feet) exhibited a pattern of movements similar to that of previous releases (Fig. 7). Another individual, female No. 52, was liberated 300 feet closer to the homesite on the fourth release than previously. Its path was oriented in the direction of the home area. It is possible that on this occasion the animal may have been responding to heavy shadows of the wooded section, which was much closer than usual due to the decreased release distance (Fig. 7).

Of the other successfully homing animals from this group, 3 were not again used in this or other experiments. Five were subsequently released a total of 15 times at different points on the golf course varying from approximately 1000 to 2200 feet from their capture sites, and in general their initial movements were more rapid than on the first release. One animal was not recovered after its second release. The remaining 4 returned to their homesites in from one to three nights on several later occasions, which suggests that they may have acquired a familiarity with a considerable portion of the golf course as a result of previous releases.

Eleven of the 42 mice (26%) from "distant" populations were recovered at the peripheral areas of the golf course in the interval of

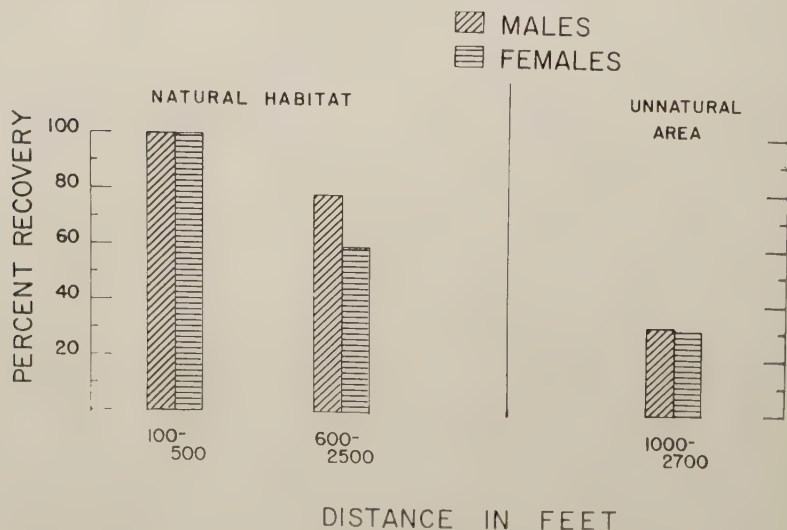


Fig. 8.—Comparative homing success of males and females in natural and unnatural habitats.

about four months after the initial liberation. Six of the 11 were released a second time at points different from the original ones. The distances ranged from approximately 1000 to 2000 feet from the last capture site. In general, these animals moved rather rapidly upon liberation though none of them was recovered again. The other 5 mice were released a second time at the original points, and their movements were also noticeably more direct. Four of these were recaptured again and released at other points on the golf course. In all, these mice were retaken on 17 occasions at different places and at intervals ranging from two days to four months between release and recapture. This suggests that the animals were wandering and had not established definite home ranges. The fifth animal was liberated a total of seven times at the same release point. Although its pattern of initial movements seemed to change with each release, this mouse, female No. 25, from a "distant" population (60 miles) consistently returned to the same trap in the northwest corner of the golf course on the same night that it was liberated (Fig. 4). On its third release at 1000 feet the animal was retaken in the usual trap within three hours after liberation. This suggests that some cotton mice that do not locate their former home ranges may settle quickly in a new area. Burt (1940), Murie and Murie (1931), and Stickel (1949) have noted a similar tendency for certain mice to remain in the vicinity of the release site.

Briefly stated, the results of the initial orientation experiments suggest that mice released in completely strange territory, whether near or distant from the home area, move in a random fashion from the release point with respect to the homesite. Animals that are successful in finding their home area and are released again at the original point may return by the previous pathway, although indirect. Their movements in subsequent trials, however, are more rapid because they are now traveling over familiar territory. Mice from distant sources that establish home ranges in the new region behave as do local animals on subsequent releases.

It is difficult to say exactly what cues the animals use for orientation under these circumstances. Vision probably plays an important role, although other sense modalities may also be involved to a significant degree.

RETENTION EXPERIMENTS

During the summer of 1959 several experiments designed to provide some indication of the degree of attachment for the home area and the role of learning and memory in homing behavior were conducted. Mice of varying previous homing experience were removed from the San Felasco and Ft. Clark study populations and retained in the laboratory for periods of time ranging from 32 to 87 days. During the period of retention the mice were kept in a small animal room which housed several other species of mammals. The mice were kept in small cages with two individuals of the same

sex per cage. Food and water were provided *ad libitum* and nesting material was supplied. After the retention period, the animals were returned to the study areas where they were liberated just prior to sundown. Some were released at different distances from the home area, while others were replaced within their former home ranges. Trapping was conducted for various periods of time afterwards to obtain data on the subsequent movements of the released animals.

The first experiment involved 12 animals (7 males, 5 females). Eight of these had been used in homing experiments at San Felasco and, therefore, were presumed to be familiar with some of the area immediately outside their trap-revealed home ranges. After laboratory isolation of from 34 to 35 days, a control group of 6 mice (2 males, 4 females) was liberated within the former home ranges of the individuals. Three females in this group had been used in homing experiments previously. Of the remaining 6 animals (5 males, 1 female) 5 were released at points that the individuals had presumably traversed in the original homing experiments. These releases included 1 male at 450 feet, 1 male and 1 female at 500 feet, and 2 males at 900 feet. A male in this group that had not been used in the original homing experiments was released at 700 feet. The distances given in each case were measured from the limits of the known home ranges to the release point. Traps were set on the grid prior to release and the area was trapped for five consecutive nights. Of the animals liberated in their former home ranges all were retrapped, the 6 mice being retaken a total of 12 times during the first trapping period. None of these individuals was taken in traps beyond the boundaries of the previously calculated home range. Only one animal was taken the first night of trapping. Five of the 6 mice liberated outside their former home ranges at distances ranging from 450 to 900 feet were retaken 11 times during the trapping period. One was retaken on the night of liberation 300 feet outside its home range but when retrapped the next night was within its former home area. All of the others were taken only within the calculated boundaries of their home ranges. The one animal not recaptured was a female liberated at 500 feet; it had successfully homed from the same distance in the original homing experiments.

Trapping in the area about six weeks later revealed that 7 of the 11 mice that were used in the retention experiment (the other 4 of the original group had been removed to the laboratory for another experiment) had remained in their original home ranges. These 7 animals were retaken 18 times during six nights of trapping, the recaptures of each being restricted to the previously calculated home range.

A second experiment was performed using 14 animals (7 males, 7 females) that were held in captivity for 32 to 34 days. One male was released within its former home range. The other animals were released outside their former home ranges as follows: 1 male and 2 females at 300 feet, 1 female and 2 males at 400 feet; 1 male at

500 feet, 1 female at 550 feet, 1 male at 650 feet, 1 male and 2 females at 700 feet, and 1 female at 900 feet. Four of the animals tested had been used in the previous experiment and therefore had been retained in the laboratory for more than 60 days with an interruption of five nights during the first experiment. Of the remaining 10 animals, 8 had never been used in any other phase of the study. Trapping was conducted for six consecutive nights beginning with the second night following liberation.

Thirteen of the 14 animals released were retrapped a total of 40 times. On the first night that traps were available, 2 mice were retaken outside their home ranges, although both animals were later (second and fourth nights) recovered in their respective home areas. All other mice were never recaptured outside of their original home ranges. Only 1 animal, a male liberated at 500 feet, was not retaken. This animal had not been used in any of the previous experiments and had a home range at the periphery of the study area which might have extended beyond the plot. Consequently, it probably had a lower probability of capture and might have returned without being recovered.

In some cases, observations were made on the initial movements of the animals at the time of liberation. On one occasion, 2 mice were released simultaneously at the same site. One of the individuals was known to have previously nested in a particular log about 10 feet from the release point, while the other mouse was 500 feet outside its former home range. The activities of the 2 mice were distinctly different, the one formerly occupying the area moved rapidly to a small hole in the log after a few seconds of hesitation, while the other mouse moved more slowly, lingering within a few feet of the observer and appeared to be examining various objects. The latter mouse was observed for about 10 minutes and was eventually lost in some fallen trees 30 feet from the release point and in the general direction of its former home area.

One mouse released in its former home range moved with little hesitation and on a direct course to a tree root 35 to 40 feet away that had been occupied during the home range studies some 15 to 16 weeks before. Another mouse released in its former home range moved a short distance away from me then turned and ran rapidly between my legs to a slight depression in the ground five feet from where it was liberated. The depression was completely covered with ground litter and did not appear to be a regular homesite. Closer examination revealed a small hole in a log buried beneath the litter. The mouse had apparently entered this hole, and its actions left the distinct impression that it had intentionally sought this refuge. The other animals liberated in this experiment were out of sight soon after release, and observations on their movements could not be made accurately.

Two more retention experiments were performed with 3 animals at Ft. Clark. The periods of isolation were 38 and 87 days. The

trapping plan, as already indicated, consisted of ten stations on either side of a sand road. Two males were used in the first experiment, 1 of the 2 having first been conditioned to homing from 950 feet and the other from 1200 feet. After 38 days of laboratory isolation, the individual conditioned to 950 feet was released at 700 feet. It was not recovered during subsequent trapping. The other male was liberated at 500 feet at a point making it necessary for it to encounter several trapping stations if it were to use the first direct route in returning home. This animal was recovered at its original homesite on the second night following release. After its first return, liberations were made at 1000, 1500, 2000, and 2500 feet. Several of these releases were in a direction that made it necessary for the mouse to encounter four trapping stations if it were to use the direct route in returning. In each case the animal was recovered at its homesite on the same night it was liberated.

This successfully homing male was again removed to the laboratory and isolated for an additional 87 days. A female conditioned to homing from 1150 feet was also retained for the same length of time. After the isolation period, both animals were released at 1000 feet on the opposite side of the road from which they were originally taken, making it necessary for the mice to cross the road if they were to regain their homesites. On the second night of trapping, both mice were recovered at the exact station where they had been caught previous to the period of isolation. Liberations at 1500 feet were then made, and both mice were back the same night. Further releases were not made, but during two nights of additional trapping, the male was retaken twice and the female once, indicating that they were persisting at their respective homesites. It is of interest to note that during the 87-day period the mice were kept in captivity the vegetational aspect of the study plot had changed markedly. A 5 to 10 foot wide strip of vegetation bordering the road had grown to approximately 5 to 6 feet from an initial height of about 1 foot, and the foliage had grown considerably denser.

The retention experiments seem to clearly indicate that the cotton mouse is able to recognize its former home range and retains a strong motivation to return to it even after a rather prolonged absence. The mice also appear capable of remembering for an equally long period of time terrain infrequently traversed and outside the normal limits of the home range.

DISCUSSION

Homing results obtained in the present study suggest, as do those for other small mammals, that cotton mice have a strong attachment to their current home range and are strongly motivated to return to this area when removed from it. The apparent lack of response to available traps outside the calculated home range observed in many instances may also be taken to indicate that a mouse responds differently to objects in the environment inside and out-

side of the familiar zone, which argues further that the familiar zone has a unique significance for the individual. Data from the retention experiments suggest that the memory of the home range and motivation to return to it are remarkably persistent when considered in relation to the average ecological longevity of six months reported by McCarley (1959) for the species in Texas.

The foregoing considerations appear to have implications in connection with our present concept of the home range of small mammals. Most attention given to the significance of the home range has emphasized the somatic aspects. That is, the home range is the area over which an animal travels in obtaining food, homesites, mates, etc., and with which it is intimately familiar and thus better able to find cover when escaping from enemies. It may be assumed that the home range not only satisfies the animal's physical needs, which might often be provided for equally well or better in other areas, but has some psychic significance. In other words, the home range offers a wide variety of associations with environmental objects to which the animal is intimately attached. Within this familiar area, the animal moves with assurance. If displaced artificially from its home area the animal may become psychologically disturbed. This state may also be accompanied by physiological changes similar to those symptomatic of stress, resulting in a search for familiar territory.

Although field-data to support this hypothesis are apparently nonexistent, laboratory experiments performed by Southwick (1959) have a bearing on the question. His results indicate that the mere transferring of adult animals to a new, but physically similar environment constitutes a relatively stressful experience. It is possible that under natural conditions wild rodents removed from the home area may show a similar response, even though the habitat in which they are released is physically similar to that of the home area. The accompanying psychological unrest may then stimulate them to look for their home areas.

Granted that small mammals have a "home sense" and are strongly motivated to return to their established home area, the question of the means by which this is accomplished must be considered. Celestial cues, including polarization patterns in the sky, the sun, stars, and moon, have been implicated in the orientation of several rather widely separated and diversified groups of animals (Carthy, 1956; Sauer, 1958). No evidence obtained in this study indicated that celestial bodies were used directly by mice in homing from the distances used, although such factors as shadows created by moonlight influenced to a certain extent the patterns and rates of at least initial movements after release. Rawson (1956) has indicated that mice successfully home under overcast skies from relatively short distances, and Bovet (personal communication), on the basis of preliminary experiments, has tentatively concluded that red mice

(*Evotomys* = *Clethrionomys*) and wood mice (*Apodemus*) do not utilize the sun in homing.

On the basis of the evidence gathered in this investigation, it is postulated that homing was accomplished in two ways: 1) random wandering in unfamiliar terrain until and if a familiar area was encountered, and 2) nonrandom movements in terrain with which the animal had some previous familiarity.

The first explanation appears to apply to the golf course experiments in which initial orientation of mice released for the first time was apparently random. In addition, the time required for recapture in homing tests was appreciably higher than in natural areas, and the proportion of recaptures from the greater distances was lower. The idea of random wandering is further supported by the observations on 4 mice whose recaptures during the several days following release suggested that the animals were unoriented with respect to a direct homing route. Animals which by chance select a pathway in the direction of their homesites may return in a short interval over a relatively long distance. Such returns may be aided by a directing influence of certain environmental features such as roads, waterways, open fields, and topographic irregularities.

Much of the homing recorded in this study is believed to have been a nonrandom activity with respect to the homesite. In other words, the animals had in actuality not been released in completely unfamiliar terrain. This view supposes that the mice are familiar to a certain extent with an area considerably larger than the calculated home range. There are several ways in which this broader knowledge of the environment may be gained. These include actually larger home ranges than are revealed by conventional methods, occasional exploratory sallies outside the home range, shifting of home ranges, and dispersal from the birthplace.

Chitty (1937) and others have suggested that small rodents may have larger home ranges than can be determined by standard trapping techniques. Such procedures as are presently employed in studying small mammal home ranges may merely give an index of the area an animal regularly encompasses in seeking its requirements. The various techniques of home range determination and the relationship between "trap-revealed" and "true" home ranges have been considered by Hayne (1949, 1950) and Stickel (1954).

Occasional trips beyond the usual home range would permit "exploratory learning" (Thorpe, 1956) and actually represent instances of "natural" homing. Such movements have been recognized in various small mammals (*e.g.*, Blair, 1940, 1943; Storer, Evans, and Palmer, 1944). Small mammals are also known to shift the home range from one period to another or expand or contract its limits (*e.g.*, Burt, 1940; Blair, 1940) and in this manner probably become familiar with additional terrain.

Dispersal from the birthplace may be a rather important way in which rodents obtain a knowledge of a larger general area than

ordinarily encompassed by the home range. In this connection, an analysis of dispersal and homing data obtained for *Peromyscus leucopus* and *P. maniculatus* by Burt (1940), Howard (1949), Stickel (1949), Dice and Howard (1951), and Murie and Murie (1931, 1932) supports the conclusion that at least part of homing success of small mammals can be attributed to familiarity with terrain acquired during dispersal. The tendency for recapture of fewer animals liberated at greater distances in homing experiments therefore seems to be related, among other things, to the dispersal of the species. The work of Levine (1960) appears to be especially significant to dispersal and homing behavior of small mammals. Levine has conclusively shown that manipulation and exposure to stresses during infancy enhances the development of normal stress responses in the adult animal. It seems likely that during dispersal from the birthplace immature mice would undergo a period of stressful experiences. Those animals dispersing the greater distances would not only learn more terrain but also would be better conditioned to a stress such as might be encountered in homing displacements. Thus, the greater the distance an animal is released from the homesite the less the chance it has had previous experience with the terrain and the lower its probability of return.

Records such as the one reported by Murie and Murie (1931) in which 1 of 23 animals released at two miles was recovered at its homesite in only 48 hours after liberation suggest that the animal may have had prior knowledge of the area gained, perhaps, during dispersal. Schleidt (1951) recovered 2 mice in about 10 to 15 minutes after releasing them at 1000 feet.

Much evidence points to the fact that in small mammals, males have a wider range of activity than females. In considering the sex differences in dispersal, the data of Burt (1940), Howard (1949), Dice and Howard (1951) and the paper of Howard (1960) appear to be significant. In general, their data show that short distance dispersal from the birthplace occurs with approximately equal frequency in males and females. Dispersal to the greater distances is, however, more frequent in males, often more than twice the percentage of females. The homing success of males and females of *P. leucopus* (Burt, 1940, and personal communication; Stickel, 1949) exhibits a close correlation with dispersal distance for that species. A sex difference in home range size with males averaging larger home ranges than females is indicated in this study and a similar trend has been reported for other species of small mammals. Barrington (1949), Pournelle (1950), and Pearson (1953) each reported a more extensive wandering habit in males of *P. gossypinus*. This evidence further suggests that males tend to be familiar with a greater area than females. If the suggestion that much of homing success in small mammals is the result of familiarity with the terrain surrounding the home area is correct, then one would expect to obtain higher homing success in males than females at least at the

greater distances. On the basis of this hypothesis, no difference in homing success of males and females released in totally unfamiliar territory would be expected. Such does appear to be the case in the golf course experiments where nearly the same proportion of males and females, 33 and 31 per cent, respectively, returned from first releases (Fig. 8). These results seem to indicate random wandering in unfamiliar territory.

The question now arises, are animals capable of learning the features of the terrain and homing pathways at an early age, and if they can, whether or not they can retain a memory of such familiarity for a prolonged period of time? Feniuk and Popova (1940), in their homing experiments with rodents, concluded that young mice (juveniles) that have not become independent of their nests do not show homing ability. The explanation of this may be two-fold. First they may lack the motivation needed for homing and second they may lack the familiarity with the terrain around their birthplaces.

This suggests that the dispersal and establishment of an adult home range are generally important for homing ability. Although the evidence is admittedly circumstantial, the fact that the same initial pathway was often followed in subsequent releases of successfully homing animals on the golf course and that movements were more rapid suggests that an animal need traverse an area one time whereupon the homing pathway is familiar and apparently learned. This is evident in the recaptures of 11 of the 12 successfully homing animals when released more than one time on the golf course and the return of several within a matter of hours. In this connection, Harrison (1958) concluded that *Rattus* was able to learn homing routes and that subsequent release of successfully homing animals at the same point of liberation results in a much higher percentage of returns. A similar trend can be found in the work of Murie and Murie (1931), Rawson (1956), Feniuk and Popova (1940), and Schleidt (1951), each of whom recorded higher homing returns from subsequent releases of successfully homing mice. The contention that learning and memory do play a role in homing ability is further supported by the present retention experiments, in which mice seemed to recognize their home ranges and were remarkably successful in homing with or without experimental experience prior to laboratory isolation. It seems possible, therefore, that cotton mice learn and retain for extended periods of time a memory of the terrain encountered during dispersal (environmental imprinting) and subsequently use this means (mnemotaxis) in homing.

The results reported in this paper by no means identify the particular sensory mechanisms utilized in homing. Visual cues may be important. Bodenheimer and Kornhauser (1955) have shown that wild mice have the ability to discern visual differences and to utilize them in learning a situation. However, other sense modalities such as auditory and chemical senses probably also play a role. It appears likely

that by utilizing the ordinary senses mice are capable of learning and retaining for prolonged periods of time a schema of their near and more distant environments and to utilize this familiarity in homing activity.

Further, it seems appropriate to suggest that psychic factors are important in a consideration of home range and homing. Based on the degree of psychological attachment to an area, small rodents may be considered to have three types of zones: 1) Territory, as defined by Burt (1943), which is the defended part of the home range; 2) Home Range, or a zone of intimate familiarity and close affinity; and 3) Life Range, or a zone of general familiarity gained as a result of dispersal, occasional wandering, and home range shifts. Homing from within the life range is assumed to be a nonrandom activity with respect to the homesites, whereas homing from beyond the life range, hence from totally unfamiliar territory, is probably by means of random wandering until familiar terrain is encountered.

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A Study of Lichen Ecology in Central Long Island, New York¹

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ABSTRACT: The epiphytic lichens of eleven forest stands in central Long Island were sampled by the random pair method and the stands are arranged in a continuum based on their epiphytic flora. This continuum exhibits certain discontinuities resulting in ecologically different segments.

The distributions of the common lichens along this continuum gradient are analyzed. Most lichens are shown to have their greatest frequency in the mature oak woods. It is suggested that if moisture and light are recognized as important factors in lichen distribution on a local level, the mature oak woods can be regarded as a point of compromise between the dry but well lighted pine-oak barrens and the moist but poorly lighted sub-climax woods.

The host-specificities of the eight common lichens for Black Oak, White Oak, and Pitch Pine are analyzed using Cole's Index of Inter-specific Association and significance tests. *Parmeliopsis placorodia* was extremely specific for *Pinus rigida*; *Graphis scripta*, *Lecanora leptyroides*, and *Parmelia saxatilis* were highly specific for Black Oak. It is noted, however, that the host-specificities in one vegetation type sometimes differ from those in other vegetation types.

This study was undertaken to expand our knowledge of the lichens of Long Island. The area is especially interesting floristically because of its unusual geographic position; the northern limit of the southeastern coastal plain element overlaps the southern limits of several northern elements. Although the central and eastern portions of the island still exhibit a rich and varied lichen flora, little collecting has occurred since the 1920's and 30's when Roy Latham was especially active. The lichens of the western portion of the island have mostly disappeared due to urbanization, and only scattered herbarium specimens and literature reports attest to their former prominence.

The specific aims of the study were (1) to determine the ecological niches of the common lichens of the area; (2) to determine the host-specificities of the common lichens for the area; (3) to set up permanent quadrats for a long term growth rate project, and (4) to secure floristic data on the lichens of central and eastern Long Island.

Since much work is still to be done on the growth rate and floristic studies, they will be discussed at some future time. This paper is confined to the ecological investigations.

¹ This study was supported by a New York State Museum and Science Service Graduate Study Honorarium for Summer Research.

² Contribution No. 60-18 from the Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan.

Acknowledgments.—I sincerely thank Dr. Eugene C. Ogden, the New York State Botanist, for helping me procure living and working facilities for the duration of the study. Thanks also go to Dr. Albert W. Herre who identified all the specimens of *Usnea* and Dr. Mason E. Hale, Jr., who identified many of my early collections. Miss Constance Nagle of the Meteorology Group at Brookhaven National Laboratory kindly supplied a compilation of climatological data. A special debt of gratitude is owed Dr. Henry A. Imshaug who verified or identified almost all the specimens collected, and who helped in the preparation of the manuscript. Many thanks are due Drs. John Cantlon, Philip J. Clark, and Thomas Eisner for their suggestions and criticisms.

HISTORY

At the turn of the century, when "botanizing" was a popular pastime and collecting a favorite hobby, Long Island became a popular area for study. In 1899, S. E. Jelliffe published "The Flora of Long Island" which listed 54 lichen taxa. In particular he studied Flushing, Jamaica, New Lots, Valley Stream, Cold Spring Harbor, Orient, Young, and Montauk (see Fig. 1). At that time, *Cladonia uncialis* was abundant in Brooklyn (now one of the most heavily populated parts of New York City) and *Cetraria islandica* dotted the now residential Richmond Hill section of Queens in New York City. Wood (1905) published additions to the lichen flora adding 18 taxa to Jelliffe's list. In 1914, Wood published a list of the lichens growing in the vicinity of New York City and included many species from Long Island.

About 1910, Roy Latham began to collect extensively in eastern Long Island. In collaboration with S. H. Burnham, he published "The Flora of the Town of Southold, Long Island" in 1914. Burnham and Latham listed 140 lichen taxa in this major contribution to our knowledge of the lichens of eastern Long Island. Latham continued his collecting and published a series of notes on his observations of *Cetraria islandica* (Latham, 1945, 1946, 1947) and one on *Cladonia alpestris* (Latham, 1949). His specimens have been widely distributed, but no résumé of his findings have been published.

The area around Cold Spring Harbor on the north shore of the island was studied by Grier in 1925. During the first few decades of the century, Raymond Torrey led many trips in connection with the Torrey Botanical Club, and published various accounts of his observations. Typical of the short, informal, but often important notes is his paper on the Rock Tripes of Long Island (Torrey, 1933).

Babette Brown Coleman's study on the epiphytes of New York (Brown, 1948) included some observations of Long Island lichens. No papers dealing with the Long Island lichen flora have appeared since 1949.

GENERAL DESCRIPTION OF THE STUDY AREA

The major vegetation types of central Long Island (Suffolk County) were sampled from Wildwood State Park on the north shore

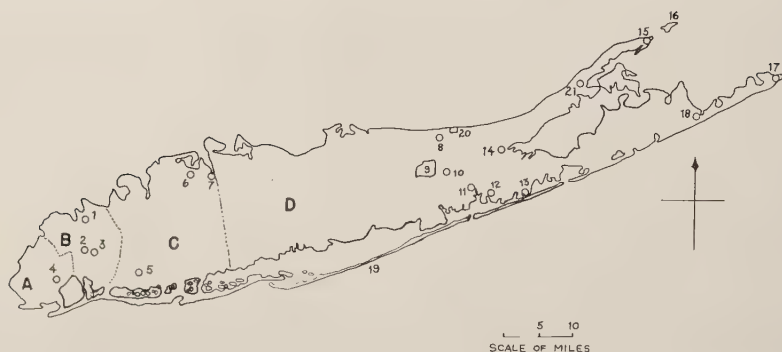


Fig. 1.—Distribution of localities on Long Island, N. Y. Counties: A—Kings (Brooklyn, New York City); B—Queens (N.Y.C.); C—Nassau; D—Suffolk. Towns, parks, etc.: 1—Flushing; 2—Richmond Hill; 3—Jamaica; 4—New Lots; 5—Valley Stream; 6—Oyster Bay; 7—Cold Spring Harbor; 8—Wading River; 9—Brookhaven National Laboratory (B.N.L.); 10—Manorville; 11—Eastport; 12—Speonk; 13—Quogue; 14—Riverhead; 15—Orient; 16—Plum Island; 17—Montauk Point; 18—Promised Land; 19—Fire Island (Sunken Forest State Park); 20—Wildwood State Park; 21—Southold.

to Westhampton Beach on the south shore, and from Brookhaven National Laboratory east to the Manorville area. Some collections were also made on the southeastern "point" of the island near Promised Land and Montauk Point, and on Fire Island near Sunken Forest State Park (Fig. 1).

Four more or less distinct terrestrial vegetation types could be recognized within the study area: sand barrens, pine-oak barrens, mature pine-oak woods, and sub-climax woods. A few bogs also occur in the area.

The vegetation of the sand barrens formed on dune-sands (Fuller, 1914), and common along the south shore, consists primarily of *Hudsonia tomentosa*,³ *Ammophila breviligulata*, and *Myrica pennsylvanica*, with a dense mat of many *Cladoniae* covering the loose sand. In the sand barren areas near the ocean, such as the one studied on Westhampton Beach in Quogue, large sand dunes dominate the area and a characteristic vegetation pattern results. A hypothetical cross-section of one of the dunes appears as depicted in Figure 2. Lichens are most abundant at the base of the lee side of the dune and in the hollows where the wind is slight. *Cladonia submitis* is by far the dominant lichen over the flats and extends far up the lee side of the dune until the brush becomes dense and little light reaches the ground. Large patches of *Cladonia boryi* and *C. uncialis* are scattered over the barrens, especially towards the base of the dune.

³ All phanerogamic nomenclature is from Fernald (1950).

Nearly circular cushion-shaped clumps of *C. boryi* were observed over large areas of totally exposed sand. Each clump was centered over the dead stump of a dune-grass plant apparently having gained its original foothold there. This may explain how slow-growing lichens can colonize a loose-sand habitat. Thus, the classical successional sequence of lichen-moss-grass-brush, is more or less reversed in this case. The hardy dune-grass is the pioneer, followed by lichens which gain a foothold on the decaying but stabilized grass stump, and this is followed by other xeric phanerogams which require some accumulated organic matter for colonization and depend on the decaying grasses and lichens for this material.

Lecidea uliginosa creates abundant tar-like patches on the bare sand of sand barrens further inland such as the one on Old Country Road near Speonk. These sand barrens are formed not on dune sand but rather on sandy outwash material from the Ronkonkoma moraine (Fuller, 1914). Associated with it are large sprawling specimens of *Cladonia cristatella*.

Pine-oak barrens represent the major vegetation type of central Long Island. They consist of mixed stands of *Pinus rigida*, *Quercus alba*, *Q. ilicifolia*, and a few other xeric oaks. The ground cover is mainly *Vaccinium* spp. No ground lichens are conspicuous with the exception of *Baeomyces roseus* which covers many bare eroded banks of the fire breaks criss-crossing the area. The soil is sandy and has little accumulated organic matter.

The pine-oak barrens grade into the mature pine-oak woods which are also common on the island. Along with large Pitch Pines and White Oaks, Black Oak (*Quercus velutina*) becomes important. As is shown below, this formation displays the richest epiphytic lichen flora. Many extensive patches of ground-dwelling *Cladoniae* such as *Cladonia subtenuis* and *C. uncialis* appear in this community

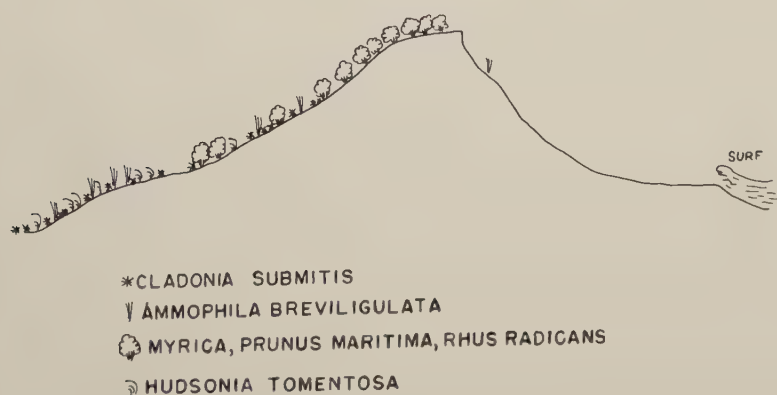


Fig. 2.—Hypothetical cross section through a "typical" sand dune at Quogue, L.I.

where there is an opening in the canopy and sunlight reaches the ground. The soil is much like that of the pine-oak barrens.

The fourth vegetation type, the sub-climax woods, was observed only on the north shore at Wildwood State Park. It has many characteristics of a typical climax forest such as sparse ground cover, thick leaf litter, and large trees. The trees, however, are mostly *Quercus velutina* and *Acer rubrum* and not typically representative of climax vegetation. Lichens are relatively rare in this formation, with a corticolous flora of mostly crustose species such as *Graphis scripta*, and without any ground lichen flora.

Three different type bogs were briefly studied. One of them (Bog A) is located on Old Country Road near Speonk (Fig. 3). It is shallow and filled with *Sphagnum* and decayed stumps, and supports many characteristic bog plants such as *Drosera rotundifolia*, *Lycopodium inundatum*, *Utricularia* spp., and *Kalmia angustifolia*. *Cladonia atlantica* was the most abundant of the several lichen species collected on the hummocks formed by the stumps.

Another bog (Bog B), formed in a gravel pit, was found just off Old Country Road near Eastport (Fig. 3). The water is extremely shallow and a tree layer is absent. The bog supports a lush growth of *Drosera rotundifolia* and *Lycopodium* spp. Around the edge of the bog, especially the northern edge, thick colonies of *Cladoniae* were



Fig. 3.—Map of central Long Island showing specific stands and areas studied.

found consisting mainly of *C. subtenuis*, *C. atlantica*, *C. uncialis*, and *C. caroliniana*. Many of the patches were growing in mats of *Polytrichum* sp. which were wet with bog water.

The third bog (Bog C), just southeast of Stand IV (Fig. 3), consists of an extensive shallow lake and a swampy adjacent area which had been used for cranberry cultivation. *Drosera* spp. and *Utricularia* spp. are abundant, and *Cladonia atlantica* and *C. subtenuis* are common at the bog edge.

CLIMATE

The climate of central Long Island falls into the "Dfa" category of Köppen's climatological classification system (Köppen, 1941). The rainfall distribution is constant throughout the year averaging four inches per month except for the dry months of June and July.

Central Long Island is rather windy with over half the days in the year having winds between 11 and 18 mph. During the summer, the prevailing winds are from the southwest; during the winter, they are from northwest.

The average temperature from May 1st to September 30th is 64.6° F, and from October 1st to April 30th, it is 39.6° F. The temperature rarely goes above 90° or below 10° F.

METHODS

Thirteen areas were selected for study including several examples of each major vegetation type. Areas I and II were treeless sand-barrens. Areas III₁, III₂, IV, V₁, V₂, VI₁, VI₂, VII, VIII, IX, and X were wooded and were studied for their epiphytic lichen flora. Each of these wooded areas will be referred to as "stands" in the following discussions. It was unfortunately not possible to restrict this study to undisturbed areas as was done in the Wisconsin studies of Hale (1955) and Culberson (1955) since almost all the wooded sections of central Long Island are "disturbed" to some degree. This study, therefore, cannot be compared with the Wisconsin studies without taking this important difference into account. An effort was made, however, to select the more undisturbed stands.

When a stand had been chosen, a 40 tree sample was taken by the "random-pair" method described by Cottam and Curtis (1949). (The correction in technique mentioned by Curtis in a later paper (Cottam and Curtis, 1955) was not used in this study.) Care was taken to avoid the edges of the woods where road effects, different light and moisture conditions, etc., might influence the data. All trees with a diameter at breast height (dbh) of 6 cm or more were studied for their epiphytic lichen flora. Observations were made on two quadrats girdling the trunk, base and breast height, in an effort to include most of the common species: (1) one quadrat was 30 cm high from the ground-level; (2) another quadrat was 40 cm high centered at 1.3 meters from the base. No notes on abundance

TABLE I.—Kulczynski's coefficient of community; each value indicates the degree of similarity between a pair of stands based on their lichen flora; the higher the coefficient, the greater is the degree of similarity.

	III ₁	III ₂	IV	V ₁	V ₂	VI ₁	VI ₂	VII	VIII	IX	X
III ₁		72	37	4	13	70	61	21	68	50	35
III ₂			38	5	13	65	75	33	81	62	50
IV				18	22	45	52	56	43	58	50
V ₁					53	5	4	14	7	24	18
V ₂						22	20	19	18	28	24
VI ₁							65	28	75	54	44
VI ₂								44	76	76	55
VII									33	46	59
VIII										68	49
IX											53

or coverage were taken in this study since the presence or absence of a particular species were the only points under consideration.

Identifications were made in the field. Any questionable specimens however was numbered and collected, and later identified in the laboratory. Because of the time factor, the only crustose lichens studied were those which could be reliably identified in the field.

CONTINUUM GRADIENT

In order to understand the distributional behavior of lichens, recent writers (Hale, 1955; Culberson, 1955) have studied the distribution of some common lichens along a "continuum" (Curtis and McIntosh, 1951) of forest types, a linear ecological arrangement of stands based on their tree composition. In those studies, the continuum was set up by an involved set of computations involving tree densities, dominance factors, and a "climax adaptation number".⁴

Because of the small number of stands examined (only eleven) and their similarity in tree composition (almost all contain *Pinus rigida*, *Quercus velutina*, and *Q. alba*), setting up a continuum according to the above method would have been impractical. The existence of a continuum can hardly be questioned, but here we have one which can best be demonstrated by including important factors that are more subtle than mere tree frequency. By analyzing the lichen composition of each stand, a continuum can be constructed which seems to reflect a linear order of ecological development. This continuum was constructed by comparing pairs of stands by Kulczynski's "coefficient of community" (Culberson, 1955). A matrix of values was constructed (Table I) from which visual analysis

⁴ A numerical value assigned to each tree species according to its autecological position in Wisconsin relative to *Quercus macrocarpa* (C.A. No. 1) which is a tree common to pioneer formations, and *Acer saccharum* (C.A. No. 10) the dominant climax forest tree.

and considerable shuffling enabled the arrangement of the stands into a linear order according to similarity and dissimilarity of the lichen composition.

The coefficient of community is a "measure of the level of similarity for any pair of communities from a set of quantitative measurements taken for both" (Culberson, 1955). It can be represented

by the formula $\frac{2w}{a + b} \times 100$ where a = the sum of the frequencies of a set of lichen species in one association, b = the sum of the frequencies of the lichen species of the other association, and w = the sum of the frequencies of the lichen species which are shared by both associations (using, of course, the lower frequency in each case as being the maximum possible shared frequency). The frequencies are expressed as percentages to permit comparisons.

By visual analysis, the following continuum series was constructed:

III₁ III₂ VI₁ VIII VI₂ IX IV X VII V₂ V₁

The most pioneer stands are at the left and the ones closest to climax are at the right.

In the process of arranging the stands into a continuum series,

TABLE II.—General characteristics of four segments of the continuum

Segment	Dominant tree or trees	Dominant ground cover	Light conditions*	Soil	Average dbh (in centimeters)		
					<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
Segment A	<i>Quercus alba</i> , <i>Pinus rigida</i>	<i>Quercus ilicifolia</i> , <i>Vaccinium</i> spp., <i>Pteridium aquilinum</i>	Excellent-good	very sandy	10.1	8.7	8.3
Segment B	<i>Pinus rigida</i> , <i>Quercus alba</i> , <i>Q. velutina</i>	<i>Vaccinium</i> spp., <i>Pteridium aquilinum</i>	Good	sandy	13.7	12.3	10.2
Segment C	<i>Quercus velutina</i>	<i>Vaccinium</i> spp., <i>Pteridium aquilinum</i>	Good	sandy	18.5	14.9	10.9
Segment D	<i>Quercus velutina</i>	<i>Parthenocissus quinquefolia</i> , <i>Viburnum acerifolium</i>	Fair	thick, moist, leaf litter		22.5	15.9

* Excellent: at least ¼ the area in open sunlight, the rest in moderate shade.
Good: less than ¼ the area in open sunlight, the rest in moderate shade.
Fair: no open sunlight falling on ground, some sunlight filtering through the trees.

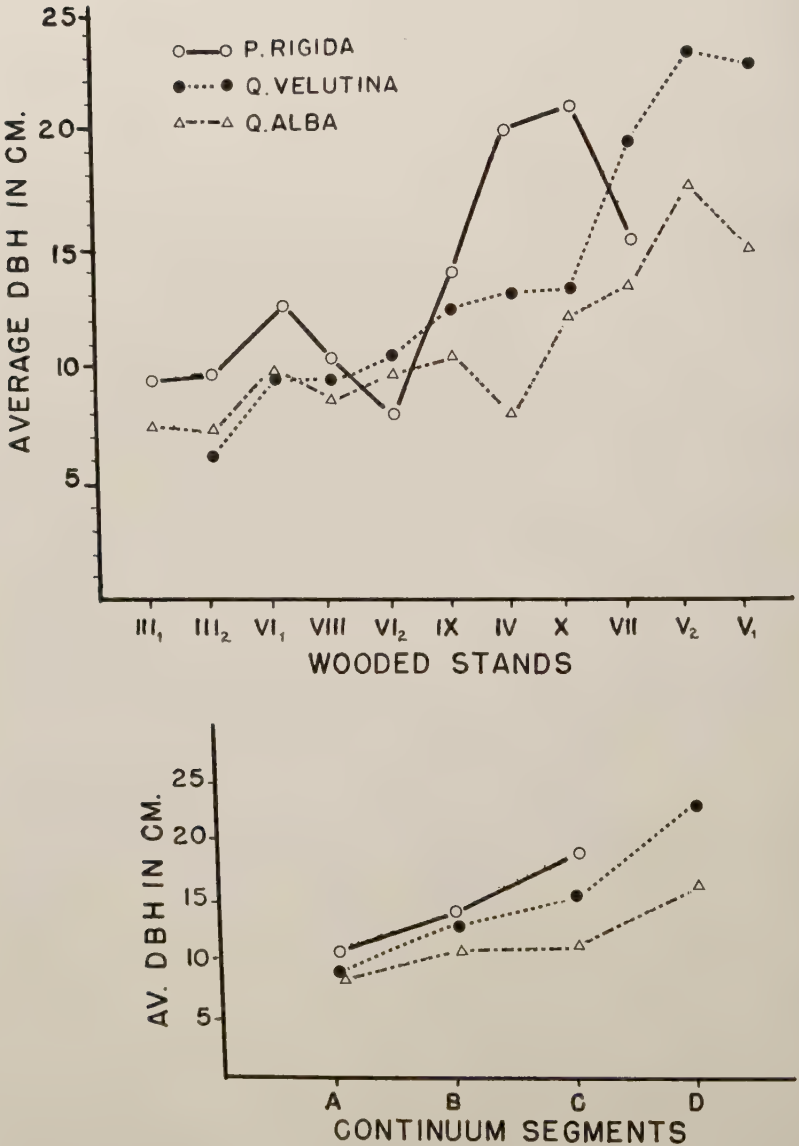
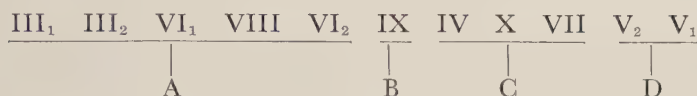


Fig. 4.—Average diameter-breast-height (dbh) of three common species of trees (*Pinus rigida*, *Quercus velutina*, *Q. alba*) along the continuum.

it was noted that the stands fell into four more or less distinct groups, almost certainly due to the small number of stands examined and the fact that the stands were originally selected to give as great a variation in vegetation type as possible. The continuum was divided into segments as follows:



It was difficult to decide on the status of Stand VI₂, but it was finally included with Segment A after much shuffling and deliberation. The other groups are rather well defined. We can classify them as follows: Segment A = pine-oak barrens, Segment B = young pine-oak woods, Segment C = mature pine-oak woods, and Segment D = sub-climax woods. The main features of these segments are

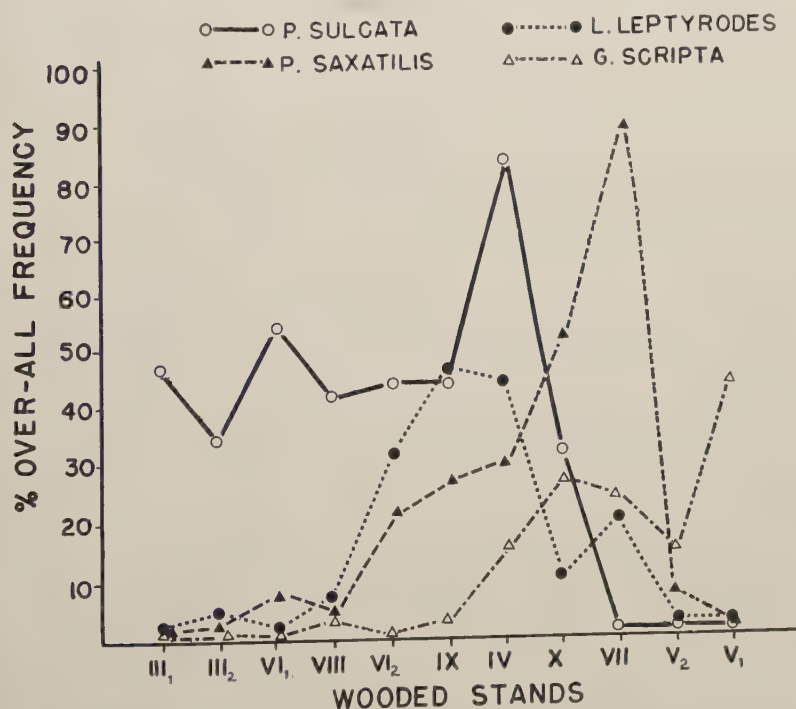


Fig. 5.—The frequencies of four common lichen species (*Parmelia sulcata*, *P. saxatilis*, *Lecanora leptyroides*, *Graphis scripta*) along a continuum of wooded stands.

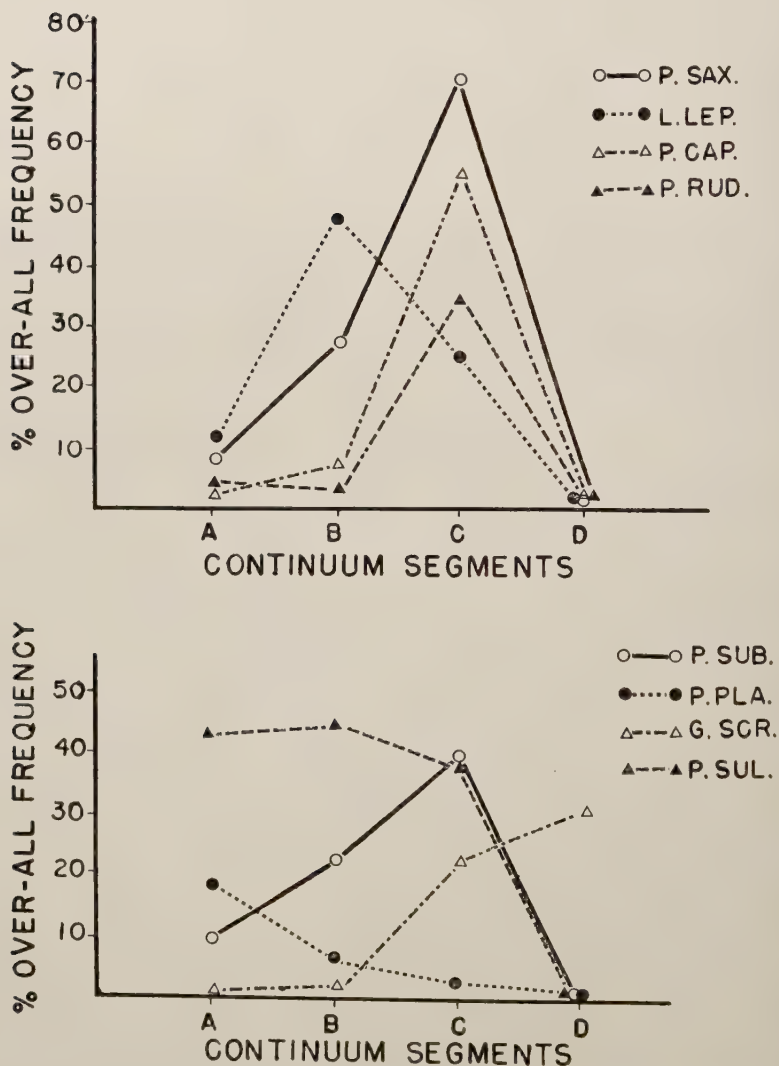


Fig. 6.—The frequencies of the eight common lichen species along the four continuum segments. (P. sax = *Parmelia saxatilis*, L. lep. = *Lecanora leptyroides*, P. cap. = *Parmelia caperata*, P. rud. = *Parmelia rudecta*, P. sub. = *Parmelia subaurifera*, P. pla = *Parmeliopsis placorodia*, G. scr. = *Graphis scripta*, P. sul. = *Parmelia sulcata*.)

summarized in Table II. Note the regular patterns which can be seen in the increase of dbh (Fig. 4), the rise and fall of light conditions, and the change of subdominants from pioneer to climax communities.

It is unfortunate that so irregular a grouping had to be made. Although the difference in number of trees represented by each continuum segment will no doubt necessitate qualifications in the conclusions drawn from its use, the arrangement gives us a more or less accurate picture of the actual situation.

Using the continuum as a framework, it is possible to plot the

TABLE III.—Frequencies of some corticolous lichens
of central Long Island

	Tree occurrence. % of 440 trees	% of total quadrat occurrences (2 quadrats per tree)	
		Basal quadrat	1.3m quadrat
<i>Cladoniae</i> *	26	88	12
<i>Graphis scripta</i>	12	23	77
<i>Lecanora subfusca</i> (group)	18	23	77
<i>Lecanora leptyroides</i>	16	24	76
<i>Lecidea anthracophila</i>	3	52	48
<i>Parmelia caperata</i>	16	56	44
<i>Parmelia perforata</i>	4		100
<i>Parmelia physodes</i> = <i>Hypogymnia physodes</i>	7	44	56
<i>Parmelia rudecta</i>	12	69	31
<i>Parmelia saxatilis</i>	22	60	40
<i>Parmelia subaurifera</i>	18	15	85
<i>Parmelia subquercifolia</i>	9	13	87
<i>Parmelia sulcata</i>	34	27	73
<i>Parmeliopsis aleurites</i>	5	20	80
<i>P. placorodia</i>	10	17	83
<i>Physcia millegrana</i>	9	7	93
<i>P. orbicularis</i>	6	52	48
<i>P. stellaris</i>	6	15	85
<i>Usnea strigosa</i>	3	22	78

* *Cladoniae* = both identified and unidentifiable material. The values here represent averages of the data collected for the epiphytic members of this genus.

frequency of the more common lichens (those with an over-all frequency of 10% or more) (see Table III) along the continuum to discover where the species are most important. Figure 5 shows the distribution of four lichens which demonstrate four major distribution patterns. When the continuum is divided into four segments (Fig. 6), we find that the distribution patterns of most of the common species fit one pattern type with a few important exceptions.

Graphis scripta frequency rises from pioneer toward climax communities. *Parmelia sulcata* does the opposite starting at a peak and dropping to zero per cent frequency in the sub-climax stands. It is interesting to note the distribution of *P. sulcata* as compared to that of the closely related *P. saxatilis*. Notice that the two patterns begin as almost exact opposites in the pine-oak barrens, then both show a peak in the mature pine-oak woods (significantly in *different* stands), and together fall to a zero point in the sub-climax (see Fig. 5).

VERTICAL DISTRIBUTION

Table III presents frequencies of lichens at the tree-base level and 1.3 meters from the base, as well as their total frequencies. From this information, we can classify the *Cladoniae* (including *C. cristatella* and the *C. chlorophaea* group) as being usually found in the basal area, and *Graphis scripta*, *Lecidea anthracophila*, *Lecanora leptyroides*,⁵ *Parmelia subquercifolia*,⁶ *P. subaurifera*, and *Parmeliopsis placorodia* as being rarely, if ever, found in the basal zone. The other species seem to show no consistent vertical distribution and probably vary in position according to the immediate light and moisture conditions. Vertical distributions of corticolous lichens and bryophytes have been studied by Charles C. Plitt (1924), Billings and Drew (1938), Hale (1952), Barkman (1958), and Brodo (1959). All these workers have emphasized the importance of moisture and light on vertical distribution of cryptogams.

MOISTURE-HOLDING CAPACITY AND pH OF BARK SUBSTRATES

Moisture-holding capacities and pH of the barks of various tree species were examined in many of the stands in which they occurred to see if the bark characteristics of any species would vary under different environmental conditions. No significant differences could be found between barks of the same species in different communities.

⁵ This species, here reported for the first time for North America, was apparently included in *Lecanora pallida* var. *angulosa* (= *L. carpinea*) by Fink (1935). *L. leptyroides* and *L. carpinea* both differ from *L. pallida* by having a C+ (orange) reaction on the apothecial disks. A cortex is present on the apothecial margin in *L. carpinea* but is absent in *L. leptyroides*.

⁶ Dr. Mason E. Hale, Jr., has recently informed me that the American material of *Parmelia subquercifolia* actually represents both *P. livida* Tayl. & *P. galbina* Ach. and that both species are represented in my Long Island material.

TABLE IV.—Cole's index of interspecific association as applied to a lichen and its supporting tree; a value of +1 indicates perfect association, and -1 indicates perfect dissociation.

	SEGMENT A			
	No. occur- rences	<i>Pinus rigida</i> 70**	<i>Quercus velutina</i> 28	<i>Quercus alba</i> 79
<i>Graphis scripta</i>	1	-1.0	-1.0	+1.0
<i>Lecanora leptyroides</i>	21	-1.0*	+ .72*	- .34
<i>Parmelia caperata</i>	7	-1.0	+ .17	+ .53
<i>P. rudecta</i>	6	-1.0	+ .61*	- .16
<i>P. saxatilis</i>	16	-1.0*	+ .35	+ .28
<i>P. subaurifera</i>	20	-1.0*	+ .07	+ .67*
<i>P. sulcata</i>	86	-1.0*	+ .56*	+ .69*
<i>Parmeliopsis placorodia</i>	37	+1.0*	-1.0*	-1.0*
	SEGMENT B			
	No. occur- rences	<i>Pinus rigida</i> 11	<i>Quercus velutina</i> 15	<i>Quercus alba</i> 13
<i>Graphis scripta</i>	1	-1.0	+1.0	-1.0
<i>Lecanora leptyroides</i>	19	-1.0*	+ .49*	+ .27
<i>Parmelia caperata</i>	3	-1.0	+ .47	+ .01
<i>P. rudecta</i>	1	-1.0	+1.0	-1.0
<i>P. saxatilis</i>	11	-1.0*	+ .71*	- .44
<i>P. subaurifera</i>	9	-1.0	+ .29	+ .18
<i>P. sulcata</i>	18	-1.0*	+ .39	+ .30
<i>Parmeliopsis placorodia</i>	3	+1.0*	-1.0	-1.0
	SEGMENT C			
	No. occur- rences	<i>Pinus rigida</i> 16	<i>Quercus velutina</i> 65	<i>Quercus alba</i> 28
<i>Graphis scripta</i>	27	-1.0*	+ .84*	-1.0*
<i>Lecanora leptyroides</i>	30	-1.0*	+ .56*	- .71*
<i>Parmelia caperata</i>	62	-1.0*	+ .33*	+ .11
<i>P. rudecta</i>	41	-1.0*	+ .36*	+ .08
<i>P. saxatilis</i>	69	-1.0*	+ .28*	+ .50*
<i>P. subaurifera</i>	49	-1.0*	+ .44*	+ .002
<i>P. sulcata</i>	46	-1.0*	+ .38*	- .55
<i>Parmeliopsis placorodia</i>	4	+1.0*	-1.0	-1.0*
	SEGMENT D			
	No. occur- rences	<i>Pinus rigida</i> 0	<i>Quercus velutina</i> 39	<i>Quercus alba</i> 16
<i>Graphis scripta</i>	25		+ .45*	-1.0*
<i>Lecanora leptyroides</i>	0			
<i>Parmelia caperata</i>	0			
<i>P. rudecta</i>	3		+1.0	-1.0
<i>P. saxatilis</i>	0			
<i>P. subaurifera</i>	0			
<i>P. sulcata</i>	0			
<i>Parmeliopsis placorodia</i>	0			

* Significance value at the five per cent level.

** Number of individual trees examined.

TABLE V.—The values presented below represent the probabilities (in per cent) of calling particular associations significant when they are in reality, insignificant.

SEGMENT A			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	60-70	80-90	40-50
<i>Lecanora leptyroides</i>	.05-.10	.00-.05	10-20
<i>Parmelia caperata</i>	5.0-10	20-30	10-20
<i>P. rudecta</i>	5.0-10	.10-.50	.95-1.0
<i>P. saxatilis</i>	.50-1.0	.10-.50	20-30
<i>P. subaurifera</i>	.10-.50	50-60	.00-.05
<i>P. sulcata</i>	.00-.05	.00-.05	.00-.05
<i>Parmeliopsis placorodia</i>	.00-.05	1.0-2.5	.00-.05
SEGMENT B			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	70-80	40-50	60-70
<i>Lecanora leptyroides</i>	.05-.10	2.5-5.0	30-40
<i>Parmelia caperata</i>	50-60	50-60	80-90
<i>P. rudecta</i>	70-80	60-70	60-70
<i>P. saxatilis</i>	2.5-5.0	.05-1.0	20-30
<i>P. subaurifera</i>	2.5-5.0	10-20	30-40
<i>P. sulcata</i>	.05-.10	5.0-10	20-30
<i>Parmeliopsis placorodia</i>	.00-.05	50-60	50-60
SEGMENT C			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	1.0-2.5	.00-.05	.10-.50
<i>Lecanora leptyroides</i>	.50-1.0	.10-.50	1.0-2.5
<i>Parmelia caperata</i>	.00-.05	.50-1.0	60-70
<i>P. rudecta</i>	.10-.50	1.0-2.5	60-70
<i>P. saxatilis</i>	.00-.05	.50-1.0	1.0-2.5
<i>P. subaurifera</i>	.10-.50	.05-.10	80-90
<i>P. sulcata</i>	.10-.50	.10-.50	5.0-10
<i>Parmeliopsis placorodia</i>	.10-.50	2.5-5.0	1.0-2.5
SEGMENT D			
	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>		1.0-2.5	.50-1.0
<i>Lecanora leptyroides</i>			
<i>Parmelia caperata</i>			
<i>P. rudecta</i>		10-20	60-70
<i>P. saxatilis</i>			
<i>P. subaurifera</i>			
<i>P. sulcata</i>			
<i>Parmeliopsis placorodia</i>			

HOST-SPECIFICITY

Some lichens have a much higher probability of being found on certain tree species than on others. In two recent papers (Hale, 1955; Culberson, 1955), this "host-specificity" was statistically demonstrated for certain lichens using Cole's Index of Interspecific Association (Cole, 1949). Cole's Index measures the degree of association between two independently varying species, in this case, the tree "host" and the lichen. The index is so constructed that a value of +1 indicates perfect association, -1 indicates perfect dissociation, and zero indicates that one species is associated with the other no more than would be expected by probability when both are randomly distributed.

Dissociation and association indicated by Cole's Index were tested for significance at the five per cent level using Chi-square and, where appropriate, Fisher's direct method (Fisher, 1950). The raw data were used in applying the tests. The Cole's Indices for the eight common corticolous lichens are presented in Table IV and the significance values presented in Table V. The data have been broken down into the four ecological groups (continuum segments) because it has been shown (Brodo, 1959) that host-specificity varies significantly under different ecological conditions.

In the present study, it is also possible to see the variation in specificity of a lichen from one group to another. Although it would be possible to construct a graph demonstrating these changes, it would lead to certain misleading conclusions because of the natural variations in the index number caused by differences in numbers of lichen and host occurrences. Instead, a set of five categories was set up based on the significance and lack of significance of the associations and dissociations over the four continuum segments. The following statements delimit the categories and present the theoretical status of the lichens as to host-specificity.

Category *a*: Lichens having a significantly high Cole's Index wherever it and the host have been found in "reasonable abundance." In this study, reasonable abundance was considered to be a frequency of five per cent or more, the figure is probably a little low, and in larger samples might be raised to 10 per cent. These species show true host-specificity in the area studied indicating possible host requirements.

Category *b*: Lichens whose indices are significantly high under some conditions and are insignificantly high or low under other conditions. These species have some specificity for the tree host, but have no clear-cut requirements for it.

Category *c*: (1) Lichens whose indices show both significant associations and dissociations, or (2) show no significant associations or dissociations at all, under various conditions. No lichens were observed to have fallen into group (1) which is as would be expected. Several species, however, could be included in group (2). Lichens in this category would seem to be most flexible in their substrate requirements, varying in degree of association with any particular tree species as the bark characteristics

such as texture, chemistry, and moisture relations change in the different stands.

Category *d*: Lichens whose indices are significantly low in some continuum segments and insignificantly high or low in others. These lichens may have some tolerance for the normally unfavorable substrate, but will occur more abundantly on other more favorable trees, if they are available.

Category *e*: Lichens having a significantly low Cole's Index wherever it and the tree are found in reasonable abundance. They have some sort of physical or physiological inability to inhabit that substrate.

Eight common lichen species were placed in the above categories according to their distribution on the three common trees (see Table VI). It must be kept in mind that an ordinarily significant association or dissociation may appear to be insignificant in an excessively small sample. (In categorizing the lichen species in Table VI, the only index values considered were those based on at least a 5% frequency of occurrence for the lichen in a given continuum segment.) For example, placing *Parmeliopsis placorodia* in category *d* with *Quercus velutina* and *Q. alba* may be misleading. There was a lack of significance in its dissociation with the oaks in Segment B where it was only found three times (a frequency of 7.5%). In a larger sample, the lichen would almost certainly have shown significant dissociations with the oaks and would have therefore been placed in category *e*. As a matter of fact, this species was never observed by the author on Long Island on any substrate other than Pitch Pine. Culberson (1954) found that in the more northern parts of the country, *Parmeliopsis placorodia* is found on *Pinus banksiana* (Jack Pine), but never on hardwoods, and this has been the personal experience of the writer in the field. However, for the most part, the table presents a good idea of the substrate behavior of the common lichens.

From Table VI, we see that besides the high specificity of *Parmeliopsis placorodia*, for Pitch Pine, *Graphis scripta*, *Lecanora leptyroides*, and *Parmelia saxatilis* are highly specific for Black Oak, although, unlike *Parmeliopsis placorodia*, they are not confined to

TABLE VI.—Degrees of host-specificity of the eight most common corticolous lichens for the three dominant trees; categories based on data in Table IV: *a* = constant positive specificity; *b* = some positive specificity; *c* = no specificity; *d* = some negative specificity; *e* = constant negative specificity.

	<i>Pinus rigida</i>	<i>Quercus velutina</i>	<i>Quercus alba</i>
<i>Graphis scripta</i>	<i>e</i>	<i>a</i>	<i>e</i>
<i>Lecanora leptyroides</i>	<i>e</i>	<i>a</i>	<i>d</i>
<i>Parmelia caperata</i>	<i>d</i>	<i>b</i>	<i>c</i>
<i>P. rudecta</i>	<i>e</i>	<i>a</i>	<i>c</i>
<i>P. saxatilis</i>	<i>e</i>	<i>a</i>	<i>b</i>
<i>P. subaurifera</i>	<i>d</i>	<i>b</i>	<i>b</i>
<i>P. sulcata</i>	<i>e</i>	<i>b</i>	<i>b</i>
<i>Parmeliopsis placorodia</i>	<i>a</i>	<i>d</i>	<i>d</i>

one tree species. In general, Black Oak appears to be the "best" substrate for the lichens in the areas studied, and *Pinus rigida* the poorest.

DISCUSSION

CONTINUUM GRADIENT

An analysis of the total flora of a stand can tell us more about the position of the stand in a continuum than can an analysis of the tree composition alone. It is also clear that the more pertinent parameters used in arranging any group of stands in a linear order, the more meaningful the order becomes. Of course, the more parameters introduced into a formula, the more cumbersome the formula becomes and calculations are made impractical. Lichen distributions have been shown in many ecological studies (Hale, 1952, 1955; Culberson, 1955; Barkman, 1958) to be influenced by many of the same environmental conditions which we would like to include in our formula, such as size of trees, available light, and humidity, besides the important factor of tree composition. By working with lichen distribution, therefore, one would be "automatically" including these parameters in the formula.

However, the use of coefficient of community values and trial and error juggling to fit the values into a linear sequence, immediately limits the number of stands one can conveniently work with. For a study such as this one covering a relatively small area with a small number of stands, especially where the tree composition is fairly constant, this method of continuum analysis is most valuable. For larger stand samples with greater variety in tree composition, the standard Curtis and McIntosh method would probably be better.

With the continuum constructed on the basis of lichen composition, lichen distribution patterns along the gradient are very similar in some ways to those seen by Hale (1955) in his study of the upland forests of southern Wisconsin. The peak in abundance of lichen species in oak woods and the sharp drop in abundance in climax forests which he observed corresponds to the peak in pine-oak woods and drop in sub-climax seen in this study. Even the exception to this general rule, that of *Graphis scripta* which rises steadily to a peak in the climax-type communities, was observed.

An important difference in the continuum, however, is in the relative position of *Quercus alba*-dominated stands. In previous studies in Wisconsin (Curtis and McIntosh, 1951; Hale, 1955), *Quercus velutina* was considered a pioneer forest tree and *Quercus alba* was considered to be a tree characteristic of woods closer to climax. In this study, the positions are reversed; that is, *Q. alba* is clearly associated with *Pinus rigida* (the ecological equivalent of *Pinus banksiana* in Wisconsin) in primitive pine-oak barrens, and *Quercus velutina* is most abundant in association with such typical climax trees as *Carya* spp. and *Ostrya virginiana*. It is possible that climatic differences between Wisconsin and Long Island or more probably differences in the biotypes of the Black and White Oaks in the two areas

produce this lack of consistency, although no definite explanation can be offered at this time.

Although it is not difficult to find patterns of distribution for most of the species studied, it is almost impossible to make any definite statements as to the causes of specific patterns. If a lichen has a host-specificity for a particular tree species, we can predict that the lichen distribution will follow more or less closely the distribution of its host (as we saw with *Parmeliopsis placorodia*). However, we can also see that specificity changes under different ecological conditions (see Table IV). These changes in specificity were noted by the writer between poorly and well-drained stands in central New York (Brodo, 1959).

It has been stated that light and humidity have an effect on lichen distribution (Plitt, 1924; Degelius, 1935; Hale, 1952; Barkman, 1958). The great abundance of lichen flora in the mature pine-oak woods probably reflects that vegetation type's position as a "compromise" point between the abundant light and extreme dryness of the pine-oak barrens and the poor light and moist conditions of the sub-climax woods. Minerals (Almborn, 1948) and salt spray (Degelius, 1935) also have their effects and may be exerting important influences on distribution especially in the sub-climax stands which are overlooking Long Island Sound (see Fig. 3). These factors are difficult, if not impossible to separate in the study area.

An interesting puzzle in distribution has been presented by two common *Parmeliae*, *P. sulcata* and *P. saxatilis*. These are closely related species with similar chemistries and morphologies. In fact, the two can only be separated by a careful examination of the thallus for the presence of isidia or soredia; *P. saxatilis* has isidia and no soredia, while *P. sulcata* has soredia and no isidia. If, in the process of speciation, the two became distinct physiologically as well as morphologically, one would expect them to inhabit entirely different niches. Figure 4 shows that for the most part, they are not found together and seem to have different ecological requirements. However, a very interesting point can be seen within continuum segment C (one of the more uniform communities). In one stand, *P. sulcata* reaches its peak, and in another it is almost absent; where *P. sulcata* is absent, *P. saxatilis* shows its peak. The two stands (IV and VII) which are within 1½ miles of each other, have very similar ecologies. There would appear to be a significant difference between the two stands, but one which so far has eluded the writer.

Graphis scripta presents a somewhat different problem. While it shows a high specificity for *Quercus velutina*, its occurrence does not closely follow that of its host particularly in continuum segment B. (See Fig. 6 and Table IV). The reasons are not clear, but it is possible that the size of the trees involved, and the resulting dissimilarities in bark characteristics, as was mentioned by Billings and Drew (1938), as well as the humidity and light conditions characteristic of progressively more "climax" forests, caused the variation.

HOST-SPECIFICITY

The data presented in this paper point to the need for caution in discussing host-specificity. It has been shown that the specificity of a lichen for a tree will vary with the ecological conditions. Thus, it is important to remember that when we speak of "the host-specificity of *Parmelia sulcata* for *Quercus velutina*," we may really mean, the specificity of the lichen for Black Oak in a dry, mature pine-oak woods, in a pine barren, etc., in central Long Island. The geographical consideration mentioned above is very important. In order to discover something about the host-lichen relations for a particular lichen species, it would be necessary to sample the forests throughout the normal range of the lichen. *Parmeliopsis placorodia* is a good case in point. The species is limited to the northeastern United States with few exceptions. In Long Island, it is found only on *Pinus rigida* which would lead us to believe that the lichen has an absolute specificity for this tree. However, as was mentioned previously, *P. placorodia* is found abundantly on *Pinus banksiana* in the northern pine barrens. It would be indeed interesting to study the host-specificity of this lichen in northern New England where the ranges of Jack Pine and Pitch Pine overlap.

The reasons for host-specificity are complicated and difficult to determine experimentally. It is believed that in certain cases, the physical and chemical bark characteristics such as moisture-holding capacity, texture, pH, and mineral composition have much to do with it (Billings and Drew, 1938; Hale, 1952 and 1955; Culberson, 1955; Barkman, 1958; Brodo, 1959). In certain highly specific lichens, especially the more primitive crustose forms, the bark may even contribute to the nutrition of the thallus (Fink, 1913; Johnson, 1940). It is impossible to make any definite statements concerning host-lichen relations at this time, although I am studying this intriguing problem to some extent.

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The Geographic Variation of *Ambystoma macrodactylum* Baird, with the Description of Two New Subspecies¹

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ABSTRACT: The taxonomic history of the salamander *Ambystoma macrodactylum* is briefly reviewed. The recently described race *A. m. croceum* is accepted. Certain differences in color and color pattern of adult animals, especially as concern the dorsal band, indicate the existence of four additional races: *A. m. columbianum* and *A. m. sigillatum*, heretofore unrecognized subspecies; *A. m. krausei* and *A. m. macrodactylum*, restricted and redefined. For each subspecies, description, distinguishing characteristics, distribution, variations or known local deviants and a list of specimens examined are presented. Sexual dimorphism of the vent is described.

Specimens of the four races are pooled into four samples and the means of 14 ratios formed from measurements and counts are compared using a completely randomized Factorial Design, the Analysis of Variance and the Individual Degree of Freedom based on the *F* distribution. A number of significant differences are demonstrated, lending additional support to the taxonomic separation of the species into the proposed races. A key to adults of the subspecies is given.

Life history data pertaining to breeding, larval development and habitat preferences are presented and compared for the various races.

INTRODUCTION

Since Baird's (1849) original description of the long-toed salamander from specimens obtained near Astoria, Oregon, the validity of the species has been widely recognized. On three occasions, certain populations of *A. macrodactylum* have been assigned species rank only to be placed in synonymy by later authorities. Peters (1882) applied the name *Ambystoma kraussii* to Flathead River, Montana specimens which he believed to differ from *macrodactylum* in dorsal band color. Cope (1883) rejected *kraussii* but described *Ambystoma epixanthum* from the South Boise River in Idaho, again on the basis of band color and certain meristic variations. Ruthven (1912) applied the name *A. stejnegeri* to four specimens supposedly collected near Bloomfield, Davis County, Iowa. Ruthven held that the Iowa animals could be distinguished from *macrodactylum* by toe length and tail morphology. Additional specimens from the Iowa locality have not been reported and it seems likely that the original locality data were in error.

More recently, Mittleman (1948) reported on the geographic variation of *Ambystoma macrodactylum* and separated the species into two allopatric races as follows: "*A. m. macrodactylum* Baird ranges

¹ Based on a thesis presented to Oregon State College in partial fulfillment of the requirements for the Doctor of Philosophy degree.

from the Columbia Plateaus province and the northern Basin and Range province in Washington and Oregon, through the Cascade-Sierra province and Pacific Border province from Calaveras County, California to southeastern British Columbia. The other race, *A. m. krausei* Peters, is known definitely from the Northern Rocky Mountain province in Idaho and Montana, and from southwestern Alberta and British Columbia as far west as Kamalloops, and probably north to Lat. 58°; it has been recorded also from Iowa."

The diagnostic features presented by Mittleman for the two races are as follows: 1) total vomerine count (67% of sexually mature *macrodactylum* with 34 or more; 75% of sexually mature *krausei* with less than 33); 2) ratio of head width to snout-vent distance (more than the value of

$$\frac{(2 \log SV)^2 - (\log SV)^2}{SV}$$

in 65% of *macrodactylum*; less than that value in 85% of *krausei* specimens); 3) ratio of head width to head length (69.5% or more in 74% of *macrodactylum* and 69.4% or less in 75% of *krausei*). In addition, the races were presumed to differ with respect to certain stable color differences.

The "subspecies" defined by Mittleman cannot be diagnosed on the basis of his "key characters." For example, although he indicates that 67 per cent of mature Oregon and Washington *macrodactylum* have vomerine counts of 34 or more, in the present study, 79.3 per cent of 222 specimens from western Oregon and Washington had 33 or less vomerine teeth. Also, in contrast to 75 per cent of Mittleman's Idaho specimens having 33 or less vomerine count, only 30.8 per cent of the 26 present study Idaho specimens had this "character." Discrepancies in the two sets of data might result from two conditions. First, and most important, Mittleman examined only a single specimen from western Oregon (Baird's type) and 75 of his 87 Oregon specimens were from Crater Lake. Second, there is a slight possibility of discrepancy because Mittleman used only specimens measuring 40 mm or more from snout to *posterior* angle of the vent and the present study used animals measuring 38 mm or more from snout to *anterior* margin of the vent.

When Mittleman's ratios were applied to specimens from the entire range of the species, they failed to prove diagnostic. Moreover, his color differences, apparently based solely on preserved material, were found to be inadequate for identification of living animals.

Recent workers have not accepted Mittleman's races. Stebbins (1951) states regarding the separation, "In my opinion there is too great overlap in the characters submitted as criteria for recognition of these races. The color differences presented are unconvincing." Schmidt (1953) omitted reference to subspecies in his checklist. Bailey (1948) criticized certain of Mittleman's statistical methods, and Mittleman (1949) has subsequently published a defense of them. Ferguson (1952a) found considerable variation between *macro-*

dactylum from western Oregon and northeastern Oregon, the latter having a more pronounced dorsal stripe after preservation, larger spots on the head, more irregular edges to the stripe and a darker ground color. In view of the confusion concerning the status of the races, the present study was initiated to re-examine the problem in light of new material obtained in the last several years.

After the present study was in progress, Russell and Anderson (1956) reported a new race, *A. m. croceum*, from near Rio Del Mar in Santa Cruz County, California. This locality is nearly four hundred miles south of the recognized coastal range of *macrodactylum* and one hundred and fifty miles southwest of the nearest Sierra Nevada populations, from which it is separated by the Great Valley of California. Although *croceum* was not included in the present study, living specimens in the possession of Russell and Anderson were examined. The pattern, color differences, and widely disjunct range clearly indicate the merit of recognizing this subspecies.

Acknowledgments.—A large number of people have contributed in one way or another to the completion of this study. The following persons have loaned specimens in their care: Mr. C. M. Beatty, Glacier National Park; Dr. Royal Bruce Brunson, Montana State University; Dr. G. Clifford Carl, Provincial Museum of British Columbia; Dr. Doris M. Cochran, United States National Museum; Dr. Philip C. Dumas, University of Idaho; Mr. J. M. Broadbent, Crater Lake National Park; Dr. Robert C. Stebbins, University of California; Dr. Kenneth Walker, College of Puget Sound. The following people contributed living specimens: Dr. Donald S. Farner, Washington State College; Dr. James Kezer, University of Oregon; Dr. David Jameson, San Diego State College; Dr. Charles W. Quaintance, Eastern Oregon College; Dr. Robert M. Storm, Oregon State College; Mr. Oliver W. Johnson, Oregon State College.

Mr. Richard Russell and Dr. James D. Anderson of the University of California kindly supplied me with a copy of their unpublished manuscript concerning *A. m. croceum* and offered many helpful suggestions as has Dr. Robert C. Stebbins of that institution. Dr. Jerome C. R. Li has very patiently advised and helped me with the statistical analyses. Dr. Richard A. Pimentel (California State Polytechnical College) and Dr. James D. Anderson read the manuscript and offered helpful suggestions. To all of these people I am most grateful.

Finally, I should like to express my sincerest appreciation to Dr. Robert M. Storm, who directed the study.

DESCRIPTION OF THE SUBSPECIES

Ambystoma macrodactylum columbianum subsp. nov.

Eastern Long-toed Salamander (Fig. 1)

Diagnosis.—An *Ambystoma macrodactylum* with: 1) a dorsal band width exceeding the internarial distance; 2) an uninterrupted band on the body that is not deeply incised; 3) band pigment on the head, snout and eyelids in the form of large, well-defined spots; 4) a combined vomerine count exceeding 33; 5) see the section on statistical analyses for other useful diagnostic characters.

Type.—USNM 142228, an adult female, collected August 3, 1956 near a small lake located 0.5 mile N. Anthony Lakes (SW¼, Sec. 7, R37E, T7S), Union Co. Oregon, (Elev. 7100 feet) by Oliver W. Johnson and Denzel E. Ferguson.

Paratypes.—USNM 142229-142246.

Distribution.—Lake County and the Deschutes drainage of Oregon, north through the Cascades of Oregon, Washington and British Columbia and east to the Bitterroot Mountains of Idaho; north through central British Columbia to S. Alaska (Fig. 2).

Description of Type (from living anesthetized specimen).— Maximum width of band on body, 5.8 mm; length from snout to anterior margin of vent, 58.3 mm; vent to tip of tail, 56.6 mm; head width, 11.2 mm; head length, 14.9 mm; length of right front leg, 15.4 mm; axilla to groin length, 27.3 mm; span of hind legs, 43.2 mm; internarial distance 3.7 mm; vomerine teeth, 36 in four groups (7, 10, 12, 7); costal grooves 13, counting one each in axilla and groin.

Dorsal stripe Wax Yellow (Capitalized color terms after Ridgway, 1912) and sharply demarcated from the black background color; the stripe is uninterrupted on the body, with a single interruption on the tail, and extends to within 3 mm of the tail tip; four patches of ground color are isolated in the band; edges of the band on the body slightly undulated with pronounced lobulations extending laterally on the tail; each eyelid provided with a large patch of band pigment; other large, well-defined patches on the head and snout; isolated patches of band color present on the lateral surfaces of the tail and upper limb surfaces; guanophores present ventral to the level of the upper eye, being smaller and fewer in number on the tail, and most abundant on the gular region, body and limbs; guanophores near the tops of the costal grooves assume the color of the band pigment; a large reddish-gold patch in the upper half of the eye; two small patches in the lower half.

Variation.—The stripe color of *columbianum* varies from bright yellow to tan, frequently appearing metallic. Although the dorsal



Fig. 1.—A specimen of *Ambystoma macrodactylum columbianum* n. ssp. from the type locality in Union Co., Oregon. Body length 58 mm; total length 107 mm.

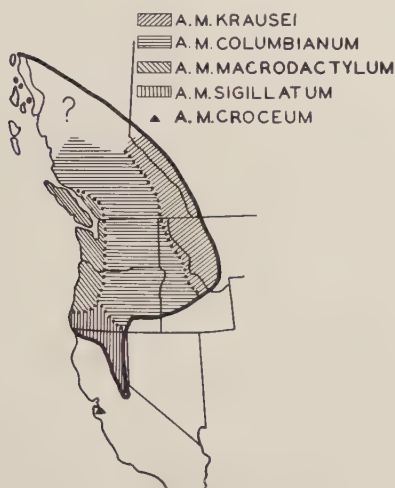


Fig. 2.—The distribution of the races of *Ambystoma macrodactylum* omitting Iowa records.

stripe is always sharply delimited from the ground color, the edges are variable, ranging from nearly parallel to irregularly indented. Large clearly defined patches of ground color are isolated in the band of some specimens but absent in most. Certain adults have a dorsal stripe more or less continuous onto the snout and the large, well-defined smooth-edged spots on the head may appear diffuse in young. The conspicuous spots of band pigment, often present on the lateral tail surfaces, are generally absent in other races. Band pigment lateral to the band and on limb surfaces is not as extensively developed as in *krausei*. The guanophores of *columbianum* are the most conspicuous found in the species. Ventral coloration may be dark chocolate in color but is lighter than the dorsal ground color.

The eye pigment is nearly always confined to the upper half of the eye, being most dense on the periphery. When pigment occurs in the lower half, it forms clumps rather than being evenly dispersed. The eye pigment of young animals is scattered throughout the eye.

Certain specimens from the Palouse area of southeastern Washington possess band characteristics differing from the typical *columbianum* pattern and approaching those of *macrodactylum*. However, the meristic characters and vomerine counts of these specimens conform to those of *columbianum*.

Specimens Examined.—IDAHO: Bonner Co. (2); Idaho Co. (6); Kootenai Co. (10); Latah Co. (18); Valley Co. (4). OREGON: Baker Co. (3); Deschutes Co. (4); Grant Co. (2); Lake Co. (3); Umatilla Co. (10); Union Co. (117); Wallowa Co. (24); Wasco Co. (14); Wheeler Co. (2). WASHINGTON: Asotin Co. (3); Chelan Co. (12); Columbia Co. (1); Douglas Co. (20); Garfield Co. (3); Grant Co. (2); King Co. (4); Kittas Co. (5); Klicki-

tat Co. (4); Lewis Co. (2); Lincoln Co. (11); Okanogan Co. (2); Pende Orielle Co. (4); Pierce Co. (3); Spokane Co. (7); Stevens Co. (5); Walla Walla Co. (1); Whatcom Co. (10); Whitman Co. (4); Yakima Co. (12). CANADA: British Columbia—Okanogan Landing (2); Kamalloops (1); Lac le Jeune (3); Telegraph Creek (1); Tetana Lake (2); Manning Park (1).

***Ambystoma macrodactylum sigillatum* subsp. nov.**

Southern Long-toed Salamander (Fig. 3)

Diagnosis.—Similar to *A. m. croceum* but with 1) bright yellow dorsal markings (Wax Yellow, Sulphine Yellow, Aniline Yellow, Lemon Chrome); 2) dorsal band often interrupted, forming smooth-edged spots or at least deeply incised, its maximum width being less than the internarial distance; 3) band pigment on head and snout in small distinct dots; 4) combined vomerine count exceeding 33; 5) see the section on statistical analyses for other useful diagnostic characters.

Type.—USNM 142212, an adult female, collected July 28, 1956 100 yards W. of the boat landing in Eagle Cove of Crater Lake, Klamath Co., Oregon, (Elev. 6170 feet) by Oliver W. Johnson and Denzel E. Ferguson.

Paratypes.—USNM 142213-142227.

Distribution.—Western Oregon south of the Calapooya divide, the southern Cascades of Oregon in the vicinity of Crater Lake, the Klamath drainage basin and south in the Sierra Nevada range to Calaveras Co., California (Fig. 2). Dr. James D. Anderson (personal communication) has recently obtained records in Tuolumne Co., thus extending the range somewhat farther south.

Description of Type (from living anesthetized specimen).—Maximum width of band on body (widest spot), 2.8 mm; length from snout to anterior margin of vent, 60.9 mm; vent to tip of tail, 54.0 mm; head width, 11.6 mm; head length, 14.9 mm; length of right front leg, 14.1 mm; axilla to groin length, 31.7 mm; span of hind legs, 40.1 mm, internarial distance 4.2 mm; vomerine teeth, 44 in four groups (7, 15, 14, 8); costal grooves 13, counting one each in axilla and groin.

Dorsal stripe Wax Yellow, sharply demarcated from the black



Fig. 3.—An *Ambystoma macrodactylum sigillatum* n. ssp. from the type locality, Crater Lake, Crater Lake National Park, Oregon. Body length 66 mm; total length 124 mm.

ground color; dorsal stripe extends from the level of the gular fold to within 10 mm of the tail tip, with three interruptions on the body and several on the tail; the stripe represented on the head and snout by tiny well-defined flecks; dorsal stripe narrow with irregular edges; stripe pigment absent on the limbs but some guanophores on the upper limb surfaces and sides of the abdomen show a yellow tinge; guanophores present on the snout and all areas ventral to a line extending through the upper eye, but are smaller and fewer in number on the tail; guanophores on sides of abdomen and upper limb surfaces tend to coalesce; an unconsolidated, silver guanoid patch in the upper half of the eye has a red tinge.

Variation. The dorsal stripe of *sigillatum* is always bright yellow, being the brightest of all the races. The stripe on the body is typically narrow and may be formed of a series of well-defined spots, or quite continuous and deeply incised. On the head, posterior to the eyes, the band pigment may form definite spots, but appears as smaller, distinct flecks or dots on the snout. The undersides are usually sparsely pigmented with a light network of melanophores and frequently appear translucent in life (with a pinkish cast, or blue where internal organs show through the body wall) and whitish gray in preservation.

The eye pigment forms a gold to silver patch, with a red tint caused by superficial blood vessels, and is confined to the upper half in adults. Small quantities of pigment may occur in the lower half of the eye in young.

A. m. sigillatum examined from the Sierras in California have a wider band than do Oregon specimens. The band may be interrupted to form a series of large, transversely arranged, smooth-edged spots. When not actually interrupted, the band may have deep undulations which nearly break through as noted by Russell and Anderson (1956). Certain specimens from the west side of Klamath Lake in Oregon resemble Sierran material. Although the Sierran population differs from typical *sigillatum*, I am inclined to view the variation as being clinal, with one extreme located near Crater Lake in Oregon and the other at the southern extremity of the species' range in the Sierra Nevada of California. Future study and more material may demonstrate the Sierran population to be distinct. At the present, in view of existing similarities and an apparently continuous geographic distribution, it seems best not to attempt separation. Russell and Anderson (*op. cit.*) recognized this problem in stating that the affinity of *croceum* seemed more likely with Crater Lake populations than with those of the Sierras.

In view of the fact that a race of newts, *Taricha granulosa mazamae*, is known to be endemic to the Crater Lake caldron, the possibility of similar local subspeciation in *Ambystoma macrodactylum* was examined. However, *sigillatum* dwelling in the caldron were indistinguishable from those in other nearby lakes and in the Rogue River Valley.

Specimens Examined.—CALIFORNIA: Alpine Co. (3); Calaveras Co. (1); Eldorado Co. (1); Plumas Co. (2). OREGON: Douglas Co. (10); Jackson Co. (27); Klamath Co. (118).

Ambystoma macrodactylum croceum Russell and Anderson
Santa Cruz Long-toed Salamander

For the sake of uniformity, the following description of the holotype of *A. m. croceum* from Rio Del Mar, Santa Cruz Co., California is included (after Russell and Anderson, 1956): "(from living anesthetized animal). Length from snout to anterior margin of vent, 57.2 mm.; from vent to tip of tail, 51.0 mm.; head width, 9.5 mm.; head length, 13.9 mm.; vomerine teeth, 33, in four groups (6, 9, 11, 7) forming a transverse arc behind the internal nares; costal grooves 13, counting one each in axilla and groin.

Ground color black, consisting of heavily concentrated melanophores; pattern on the back a series of eleven small orange patches; this light pigment represented by tiny dots on head and a nearly continuous stripe along crest of tail; guanophores absent dorsally, concentrated as a band of silvery flecks dorsolaterally along a line connecting the limb insertions and extending forward onto the upper surfaces of cheeks and forelimbs; guanophores fewer on hind limbs and lateral surfaces of tail, widely scattered on belly; upper half of eye with a guanoid patch given a pinkish cast by associated blood vessels; this eye color lost after preservation".

Identifying characteristics for *croceum* are a dull orange dorsal band (between Pekinese and Raw Sienna), a tendency for the band to be broken up into a number of discrete spots, and a reduced dorsal head pattern which consists of scattered dots, that are often absent anterior to the eyes.

The race *croceum* is known only from Santa Cruz County, California (Fig. 2).

Although *croceum* was not studied, it should be pointed out that it could only be confused with *sigillatum*, and only then if distribution was unknown for a salamander in question. The two races are easily separated by band color (Raw Sienna in *croceum*, yellow in *sigillatum*) and a more discontinuous band and darker ground color in *croceum*.

Ambystoma macrodactylum krausei Peters
Northern Long-toed Salamander (Fig. 4)

On the basis of the present study, the name *krausei* is restricted to *A. macrodactylum* having the following distribution: Bitterroot Mountains of eastern Idaho, throughout western Montana and north through western Alberta and eastern British Columbia (east of the Selkirk Mountains) to Jasper National Park (Fig. 2). Specimens from Valley and Idaho Counties in central Idaho show a *krausei* influence in having a band more continuous onto the head and are considered to be intergrades with *columbianum*.



Fig. 4.—A specimen of *Ambystoma macrodactylum krausei* from 11 miles east of Eisenhower Forks, Banff National Park, Alberta, Canada. Body length 57 mm; total length 98 mm.

The following description pertains to a representative specimen of *krausei* (from living anesthetized animal): Oregon State College MNH 3580, an adult male collected July 7, 1955 about 11 miles E. of Eisenhower Forks, Banff National Park, Alberta, Canada by Denzel E. Ferguson.

Maximum width of band on body, 3.2 mm; length from snout to anterior margin of vent, 49.3 mm; vent to tip of tail 47.7 mm; head width, 8.8 mm; head length, 12.2 mm; length of right front leg, 13.9 mm; axilla to groin length, 30.2 mm; span of hind legs, 40.1 mm; internarial distance 3.0 mm; combined vomerine count, 31; costal grooves 12, counting one each in axilla and groin.

The dorsal band is Aniline Yellow at midbody becoming darker on the ridge of the tail. Near the stripe at midbody, the ground color is between Aniline Black and black. The dorsal stripe is narrow, starting at the mouth line and extending to within 2 mm of the tail tip with but a single interruption on the tail. The stripe is expanded immediately posterior to the eyes at which point a large patch of ground color is isolated within the band. Each eyelid has a large well-defined spot of band pigment. The edges of the band are nearly parallel and abruptly separated from the surrounding ground color. On the body, a dozen or so patches of band color are isolated lateral to the band proper, and many large distinct patches of band pigment are present on the dorsal surfaces of both fore and hind limbs.

Guanophores are present on the sides of the snout and lateral

surfaces of the body (up to the level of the dorsal edge of the eye), becoming more sparse laterally on the tail. Guanophores on the body near the band assume a tinge of the band color. Smaller guanophores are abundant ventrally and are sometimes clumped to form larger white patches. Guanophores are lacking on the dorsal limb surfaces but present on the lips of the vent.

Variation.—The ground color of *krausei* is often conspicuously darkened adjacent to the band. Isolated ground color is seldom seen in the band, although the dorsal stripe of two specimens of a series from Glacier National Park, Montana, is broken into spots similar to those of *sigillatum* and *croceum*. Guanoid pigment of the eye is silver or gold with a red tint and is often absent entirely. In young, the pigment may appear gray and is evenly dispersed throughout the eye. *Krausei* is very dark ventrally due to a dense melanophore network. Ruthven's type for *stejnegeri* has been examined and found to fit *krausei* as here described.

Identifying characters for *krausei*: 1) band continuous onto the snout and widest in the vicinity of the eyes; 2) band yellow and uninterrupted; 3) large patch of band color on each eyelid; 4) band narrow and the edges nearly parallel; 5) combined vomerine count less than 34; 6) see statistical analyses for other characters of value.

Specimens Examined.—IOWA: (?) Davis Co. (1). MONTANA: Flathead Co. (21); Glacier Co. (1); Lake Co. (8); Missoula Co. (30); Ravalli Co. (18); Sanders Co. (8). CANADA: Alberta—Eisenhower Forks (3). British Columbia—Cranbrook (1); Echo Lake (8); Kootenai Crossing (5); Mount Monashee (10).

Ambystoma macrodactylum macrodactylum Baird

Western Long-toed Salamander (Fig. 5)

The nominate race, as here defined, includes *A. macrodactylum* populations west of the Cascade Mountains, extending from the Calapooya divide in Oregon, north through western Oregon and Washington and along the coast of British Columbia to a point opposite the northern tip of Vancouver Island, including Vancouver Island and other offshore islands (Fig. 2).

The following is a description of a representative specimen of *A. m. macrodactylum* (from living anesthetized animal): Oregon State College MNH 3985, an adult male collected April 10, 1956 near Corvallis, Benton Co., Oregon by Denzel E. Ferguson. Maximum width of band on body, too diffuse and indistinct to measure; length from snout to anterior margin of vent, 50.3 mm; vent to tip of tail, 47.4 mm; head width, 9.0 mm; head length, 11.4 mm; length of right front leg, 15.3 mm; axilla to groin length, 26.0 mm; span of hind legs, 39.8 mm; internarial distance, 2.92 mm; combined vomerine count, 30; costal grooves, 13, counting one each in axilla and groin.

The dorsal band is between Citrine and Dark Citrine at mid-body, changing to Dull Citrine on the tail. The ground color at

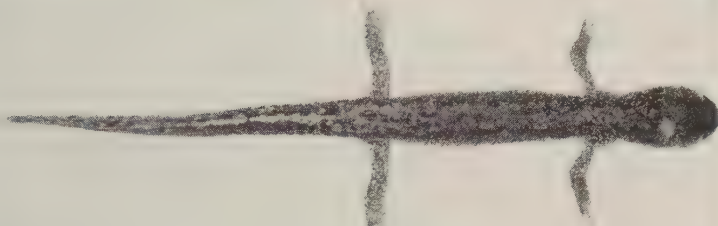


Fig. 5.—An example of *A. m. macrodactylum* collected near Corvallis, Benton County, Oregon. Body length 56 mm; total length 104 mm.

midbody approaches Dark Quaker Drab. The band is very diffuse in appearance, and forms a gradual transition into the ground color making it impossible to say where one begins and the other stops. A tint of ground color is evident throughout the band. Anterior to the gular fold, the stripe is absent, but represented by a very diffuse "wash" of band pigment, which consists of extremely irregular scattered flecks. Band pigment on the eyelids is also of this diffuse nature. The edges of the band are formed by a dispersion of band pigment, similar to that described for the head, which almost imperceptibly changes into a dense concentration of guanophores on the lateral surfaces of the body. These guanophores are extremely numerous coalescing in a manner to give the sides a solid whitewashed appearance. This dense concentration of guanophores extends ventrally from the level of the eyes to a line connecting the fore and hind limb bases, below which they gradually become fewer and separated. Scattered guanophores appear on the gular region, limb surfaces and lower halves of the lateral tail surfaces. The eye pigment consists of green or red tinged golden flecks, mainly in the upper half of the eye (most concentrated near the edge of the pupil), but with scattered patches in the lower half as well.

Variation.—In life, the band of adult *macrodactylum* is drab (usually Dull Citrine or Dark Citrine) but often approaches bright yellow in recently metamorphosed young. In aquatic, breeding adults and after preservation, the band of Willamette Valley specimens may be so indistinct as to appear absent at a first glance. Band pigment is frequently absent from the upper limb surfaces and never conspicuous if present. Guanophores extend higher on the sides in this race than in others, and fewer melanophores give it a lighter ground coloration, especially on the ventral aspects. Eye pigment of young is dispersed throughout the eye.

Some specimens of *macrodactylum* from the Olympic Peninsula area of western Washington have a more distinct band, approaching that of *columbianum*. However, their meristic characteristics and

vomerine counts are those of *macrodactylum*. The coloration and pattern of Baird's type, although difficult to discern, show a tendency toward *columbianum*. A possible explanation may be a *columbianum* gene flow through the Columbia River Gorge, since some larvae and adults are no doubt washed downstream and adults accidentally transported with debris. A single specimen from Columbia Co., Oregon displayed similar evidence of the *columbianum* race in its band characteristics.

Identifying Characters for macrodactylum.—1) dorsal stripe dull in color (citrine), appearing very diffuse on the head, snout, eyelids and edges of the band; 2) guanophores reaching to the dorsal extremities of the costal grooves and coalesced to give the sides a whitewashed appearance; 3) light gray ground color with tinges of brown in preservation; 4) combined vomerine count less than 34; 5) head short and narrow; 6) see statistical analyses for other characters of value.

Specimens Examined.—OREGON: Benton Co. (101); Clatsop Co. (1, Baird's type); Columbia Co. (1); Lane Co. (21); Linn Co. (100); Polk Co. (4). WASHINGTON: Callam Co. (8); Cowlitz Co. (4); Gray Harbor Co. (7); Island Co. (1); King Co. (6); Kitsap Co. (2); Lewis Co. (5); Mason Co. (8); Pierce Co. (35); Skamania Co. (8); Snohomish Co. (2); Thurston Co. (2). CANADA: British Columbia—Hope (12); Vancouver Island (4); Huntingdon (1).

INTERGRADATION

Exact statements concerning the nature and extent of intergradation between the races of *Ambystoma macrodactylum* must await additional study based on intensive collecting in suspected zones of contact. However, examination of available collections has helped to clarify the problem in at least a few significant areas. The subspecies *sigillatum* and *columbianum* are known to intergrade where they meet along a fairly restricted zone through Klamath and Lake Counties in south-central Oregon (Fig. 2). Specimens from this area possess the wider dorsal stripe of *columbianum* but have the characteristic interrupted pattern of *sigillatum*.

Intermediates between *sigillatum* and *macrodactylum* are not known. Present data indicate their geographic ranges to be disjunctly allopatric, the Calapooya Divide, in west, central Oregon, being the possible point of separation.

No *macrodactylum* records are available from the western slope of the Oregon and Washington Cascade Mountains, and it is doubtful that they will be forthcoming. However, the distribution of *columbianum* extends up the eastern slope to the crest of the range. This apparently disjunct pattern of distribution would appear to preclude genetic interchange between *macrodactylum* and *columbianum* along the Cascade barrier. However, as mentioned above, *columbianum* influence via the Columbia River Gorge is apparent in *macrodactylum* populations from areas along the lower Columbia River in north-

western Oregon. Specimens from southwestern British Columbia, along the Frazier River drainage in the area east of Vancouver, also appear to be intergrades between these two races.

A fairly broad zone of intergradation between *columbianum* and *krausei* runs parallel to the Bitterroot and Selkirk ranges, beginning in central Idaho and extending northward through western British Columbia. Salamanders from Bonners Ferry, Idaho are definitely intermediates and impossible to allocate to subspecies. The identity of the subspecies occupying northern British Columbia and southern Alaska is not known for certain, there being only a few poorly preserved specimens available from the region. Those examined more closely approach *columbianum* than any other race.

LARVAE AND YOUNG

Large numbers of *columbianum* and *macrodictylum* larvae were examined but consistent differences were not found. However, there is a tendency toward a darker coelom lining and a higher gill raker count in *columbianum*. Immatures cannot be assigned to their subspecies on the basis of diagnostic adult characters. Recently metamorphosed young of all subspecies exhibit bright dorsal stripes (Strontium Yellow, Wax Yellow, Oil Yellow, Amber Yellow, Olive Ochre, Deep Colonial Buff), important band characteristics are not evident, and vomerine counts are not reliable.

SEX DETERMINATION

The sex of breeding long-toed salamanders is usually established by examination of the vent. However, in rare instances, dissection and examination of the gonads might be necessary. In general, the vent of breeding males is extremely bulbous due to enlargement of the cloacal lips, while the cloacal lips of females form a much smaller cone-like protuberance. The vent of the male is more heavily pigmented with melanophores and has a long opening that is lined by protuberant flaps of tissue bearing rows of papillae. In females the cloacal lip pigment is sparse or lacking, the vent is shorter and the inside lining is grooved or ridged in place of being papillate. Vent dimorphism is considerably more pronounced in *macrodictylum* than in *columbianum* or *sigillatum* but only slightly more so than in *krausei*. Dr. James D. Anderson (personal communication) has pointed out that *croceum* shows strong vent dimorphism, approaching that of *macrodictylum*.

STATISTICAL ANALYSES

Only animals measuring 48.5 mm or more snout to vent were used in the statistical analyses. Measurements were taken with Vernier calipers and read to the nearest one-tenth millimeter, except as otherwise specified below. Contorted or poorly preserved animals were forcibly flattened, if possible, or otherwise omitted. The following information was taken from each specimen:

1) length of right front leg—the distance from the tip of the longest toe to the point of limb attachment to the body;

2) head length—the distance from the tip of the snout to the gular fold;

3) snout-vent length—the distance from the tip of the snout to the anterior end of the cloacal orifice. Mittleman (1948) believed that sexual maturity was achieved at 38 mm in males and about 39 mm in females, his measurements being the conventional snout-vent distance (from tip of the snout to the posterior angle of the vent opening). However, such measurements, if valid at all for indicating sexual maturity, apply only to animals which metamorphose during the first year. Individuals from certain areas, i.e., Crater Lake, may require two years in the larval state and consequently reach a larger size before leaving water (Kezer and Farner, 1955). These recently metamorphosed individuals commonly exceed 40 mm snout-vent length (*sensu* Mittleman) and yet retain gill stubs, a larval tail fin, lack a dorsal band and retain larval proportions. It appeared that a minimum snout-vent length of 48.5 mm would assure that the majority of the specimens were sexually mature and of adult proportions. It is of interest that Dr. James D. Anderson (personal communication) has recently pointed out that 48.5 mm is also the approximate size (average) of sexual maturity in *croceum*;

4) head width—maximum head width, usually just posterior to the eyes;

5) internarial distance—the distance between the medial margins of the external nares. This measurement was made with a calibrated eyepiece micrometer under a binocular dissecting microscope, each unit being equivalent to 0.083 mm;

6) interorbital distance—the distance between the anterior corners of the eyes, obtained in the same way as the internarial distance;

7) lens size—the greatest diameter of the extracted right eye lens, measured with the eyepiece micrometer, each unit equivalent to 0.023 mm. The lens has previously been used in salamander taxonomy by Hendrickson (1954) in studying the genus *Batrachoseps*;

8) total length—from the tip of the snout to the tip of the tail, taken with the animal on its back and flattened;

9) tail length—from the posterior margin of the cloacal orifice to the tip of the tail;

10) per cent of total length in tail—a ratio obtained by dividing the tail length by the total length;

11) axilla to groin distance—from the axilla or pit of the forearm to the groin, measured with the animal on its back and flattened;

12) span of hind legs—the distance from the tip of the longest toe of one hind foot to the tip of the longest toe on the other hind foot, measured with the animal on its back, the limbs at right angles to the body and adpressed to the table surface;

13) width of band—the widest portion of the band when rela-

tively unbroken, measured between the fore and hind legs at right angles to the body, or if broken into spots, the width of the widest spot. This measurement could not be obtained from many individuals of the race *macrodictylum*, their bands being too diffuse or indistinct to measure;

14) combined vomerine count—the number of teeth in the four series added together to obtain a single total count.

All subspecies, excepting *croceum*, were subjected to statistical analyses to determine if meristic differences could be correlated with geographic origin and pattern variation. For purpose of analysis, animals from each of the four races studied were pooled (*i.e.*, grouped) to form four samples. The several measurements tested were employed as ratios, a method used by Dunlap (1955) in working with frogs. Ratios were formed by dividing the larger number into the smaller. In one instance, per cent of total length in tail/ combined vomerine count, the two numbers varied as to which was larger. The vomerine count was usually the smaller figure.

The following fourteen ratios were tested: head length/ snout to vent; head length/ axilla-groin; head length/ per cent of total length in tail; head length/ length of right front leg; head width/ axilla-groin; head width/ snout to vent; head width/ head length; band width/ head width; band width/ interorbital distance; interorbital distance/ band width; interorbital distance/ axilla-groin; axilla-groin/ span of hind legs; length of right front leg/ axilla-groin; per cent of total length in tail/ combined vomerine count. In addition, the following ratios involving lens diameter were tested only between *columbianum* and *macrodictylum*: per cent of total length in tail/ lens diameter; axilla-groin/ lens diameter; span of hind legs/ lens diameter; snout to vent/ lens diameter; lens diameter/ total length. All ratios involving lens diameter were formed with the number of eyepiece micrometer units (usually a number between 50 and 100, each unit equivalent to 0.023 mm.) rather than the value obtained by conversion to millimeters. This procedure was suggested as a method of conserving digits by Dr. J. C. R. Li, biometrician at Oregon State College. Since only three digits beyond the decimal were saved in the formation of ratios, the number of micrometer units, being a large whole number, provided three useful digits. The converted millimeter value, being very small, provided only one or two useful digits beyond the decimal. Too few lens diameter measurements were available for *krausei* and *sigillatum*, these races being studied largely from borrowed material from which lenses were not usually removed.

The type of test used is based on the completely randomized Factorial Design and utilizes the Analysis of Variance based on the *F* distribution (Li, 1957). An equal number of males and females is used for each race, but the sample size for each race frequently differs. For every ratio three factors are tested: 1) race; 2) sex; 3) sex x race (interaction). A mean square value is calculated for

each of these factors, which when divided by the error mean square (pooled variance) yields an F value. The 1 per cent significance level is utilized in all tests.

The critical region is determined by the number of degrees of freedom, which ranges from 3 and 128 to 3 and 416 for race and sex $\times$ race and from 1 and 128 to 1 and 416 for sex. The number of degrees of freedom depends upon the number of animals used in a particular test. Since the F values change only slightly between 120 and infinity, a value midway between that for 120 and infinity degrees freedom was selected to establish the critical regions at $F > 3.85$ for race and race $\times$ sex and $F > 6.75$ for sex. Since all of the calculated F values fall either well outside or inside the critical region, no case is disputable, and further refinement of the critical region is unnecessary. The critical region for all tests involving lens diameter (*columbianum* vs. *macrodictylum*) is $F > 6.75$ for race, sex and interaction.

When an F value for race exceeds 3.85 and is, therefore, significant, it indicates that the mean for the ratio being tested differs in two or more of the populations from which the samples were drawn and that such a difference would only be indicated in 1 of 100 times by chance. If an F value for race proves significant, the Individual Degree of Freedom is used to determine between which of the races the indicated difference is to be found. Thus, further F values are obtained by comparing *columbianum* $\times$ *macrodictylum*, *columbianum* $\times$ *krausei*, *columbianum* $\times$ *sigillatum*, and *macrodictylum* $\times$ *sigillatum*. These tests are also at the 1 per cent significance level, with the critical region being $F > 6.75$.

A significant F value for sex indicates that sexual dimorphism is exhibited in the ratio being tested. A significant F value for interaction (sex $\times$ race) indicates that sexual dimorphism is not the same within one or more of the four races.

Table I gives the sample mean (M), the sample mean for each sex ($\bar{M}$, $\bar{M}$) and the number of specimens tested for each ratio. All F values obtained in the tests, the significant ones being indicated by an asterisk(*), are given in Table II.

STATISTICAL SUMMARY

Race.—The means of all 14 ratios tested for race were found to differ significantly. The source of variation is indicated in the following table:

Source of Variation	Differences (Significant F values)	Similarities (Non-signifi- cant F values)	Number Possible
<i>columbianum</i> $\times$ <i>macrodictylum</i>	10	4	14
<i>columbianum</i> $\times$ <i>krausei</i>	11	3	14
<i>columbianum</i> $\times$ <i>sigillatum</i>	9	5	14
<i>macrodictylum</i> $\times$ <i>sigillatum</i>	12	2	14

The means of five ratios involving lens diameter of *columbianum* and *macrodictylum* all were found to differ significantly.

The ratio head width/ head length is of particular interest for it was one which Mittleman claimed would differentiate his proposed subspecies. However, the present statistical data show that it fails to separate *krausei* and *columbianum* (*krausei* and *macrodactylum*, *sensu* Mittleman). Yet the ratio *does* separate *columbianum* from both *macrodactylum* and *sigillatum*, all three of which were included in the subspecies *macrodactylum* in Mittleman's treatment. The present statistical evidence clearly demonstrates many marked differences in comparisons made between *macrodactylum* and both

TABLE I.—Means and sample sizes for the samples treated in the statistical analyses

Ratio		Subspecies			
		<i>macro-</i> <i>dactylum</i>	<i>colum-</i> <i>bianum</i>	<i>sigil-</i> <i>latum</i>	<i>krausei</i>
Head length/ snout-vent	M	.219	.238	.239	.227
	♀ M	.217	.238	.238	.231
	♂ M	.221	.237	.239	.223
	N	160	126	100	38
Head length/ axilla-groin	M	.400	.454	.463	.431
	♀ M	.391	.449	.454	.429
	♂ M	.410	.459	.472	.433
	N	158	120	100	38
Head length/ per cent of total length in tail	M	.245	.284	.288	.249
	♀ M	.251	.298	.299	.263
	♂ M	.239	.270	.277	.235
	N	124	98	96	32
Head length/ length of right front leg	M	.801	.816	.803	.780
	♀ M	.855	.841	.832	.823
	♂ M	.747	.791	.775	.737
	N	156	120	100	38
Head width/ axilla-groin	M	.314	.345	.360	.329
	♀ M	.304	.336	.352	.315
	♂ M	.325	.353	.368	.343
	N	158	120	100	38
Head width/ snout-vent	M	.172	.180	.186	.173
	♀ M	.169	.177	.185	.170
	♂ M	.176	.183	.187	.177
	N	160	126	100	38
Head width/ head length	M	.788	.760	.779	.765
	♀ M	.779	.744	.776	.738
	♂ M	.797	.775	.783	.793
	N	160	126	100	38
Band width/ head width	M	.479	.496	.289	.405
	♀ M	.477	.509	.298	.405
	♂ M	.482	.483	.281	.405
	N	76	118	94	36

TABLE I.—(continued)

Band width/ interorbital distance	M	.754	.795	.460	.662	
	♀ M	.755	.815	.478	.698	
	♂ M	.754	.774	.441	.627	
	N	76	118		92	36
Internarial distance/ band width	M	.776	.755	1.345	.915	
	♀ M	.766	.734	1.312	.877	
	♂ M	.785	.775	1.378	.953	
	N	76	118		92	36
Interorbital distance/ axilla-groin	M	.195	.216	.229	.212	
	♀ M	.189	.211	.223	.204	
	♂ M	.202	.221	.236	.220	
	N	158	120		100	38
Axilla-groin/ span of hind legs	M	.760	.674	.655	.704	
	♀ M	.814	.692	.684	.753	
	♂ M	.706	.656	.626	.655	
	N	156	118		98	38
Length of right front leg/axilla- groin	M	.503	.559	.578	.551	
	♀ M	.458	.538	.547	.511	
	♂ M	.549	.581	.609	.591	
	N	156	118		100	38
Per cent of total length in tail/com- bined vomerine count	M	1.712	1.266	1.172	1.615	
	♀ M	1.595	1.212	1.147	1.484	
	♂ M	1.829	1.321	1.196	1.746	
	N	124	96		96	32
Per cent of total length in tail/lens diameter	M	.677	.538			
	♀ M	.658	.514			
	♂ M	.695	.561			
	N	88	44			
Axilla-groin/ lens diameter	M	.412	.338			
	♀ M	.424	.346			
	♂ M	.400	.331			
	N	114	44			
Snout-vent/ lens diameter	M	.750	.655			
	♀ M	.760	.664			
	♂ M	.741	.646			
	N	114	44			
Lens diameter/ total length	M	.654	.785			
	♀ M	.673	.791			
	♂ M	.635	.779			
	N	88	44			
Span of hind legs/ lens diameter	M	.538	.511			
	♀ M	.514	.503			
	♂ M	.562	.519			
	N	112	44			

TABLE II.—*F* values obtained in comparing sample means of ratios tested

SOURCE OF VARIATION																	
RATIO:		Race		<i>columbianum</i> x <i>macrodactylum</i>		<i>columbianum</i> x <i>krausei</i>	<i>columbianum</i> x <i>sigillatum</i>	<i>macrodactylum</i> x <i>sigillatum</i>	Sex	Sex x Race	Error	Total					
		F	DF	F	DF	F	DF	F					DF				
Head length/ snout vent		73.83*	3	156.90*	1	21.47*	1	.35	1	152.45*	1	.23	1	2.52	3	416	423
Head length/ axilla-groin		86.90*	3	164.03*	1	12.72*	1	3.77	1	201.58*	1	18.50*	1	.74	3	408	415
Head length/ T.L. in tail	%	91.01*	3	161.33*	1	57.86*	1	1.51	1	193.94*	1	70.01*	1	2.52	3	342	349
Head length/ Rt. F. Leg	L.	4.86*	3	5.53	1	13.40*	1	3.13	1	4.97	1	220.08*	1	7.95*	3	406	413
Head width/ axilla-groin		71.14*	3	93.55*	1	10.77*	1	19.44*	1	191.40*	1	58.68*	1	.70	3	408	415
Head width/ snout-vent		50.09*	3	51.41*	1	17.16*	1	20.99*	1	131.76*	1	41.62*	1	14.71*	3	416	423
Head width/ head length		7.34*	3	20.17*	1	.34	1	7.66*	1	1.65	1	19.97*	1	2.25	3	416	423
Band width/ head width		95.53*	3	1.44	1	25.68*	1	250.11*	1	169.74*	1	1.53	1	.48	3	316	323

TABLE II.—(continued)

Band width/ interorbital distance	F DF	97.93* 3	3.41 1	21.99* 1	264.63* 1	164.98* 1	4.27 1	.52 3	314	321
Internarial/ band width	F DF	120.61* 3	.34 1	12.08* 1	307.37* 1	230.25* 1	3.03 1	.19 3	314	321
Interorbital/ axilla-groin	F DF	82.34* 3	93.75* 1	1.06 1	32.84* 1	232.47* 1	54.01* 1	.35 3	408	415
Axilla-groin/ Span hind legs	F DF	105.25* 3	189.00* 1	9.71* 1	7.34* 1	252.33* 1	217.09* 1	12.49* 3	402	409
L. Rt. F. Leg/ axilla-groin	F DF	77.03* 3	121.58* 1	1.06 1	10.71* 1	195.26* 1	289.70* 1	7.95* 3	404	411
% T.L. in Tail/ T. Vomer. Count	F DF	56.41* 3	81.55* 1	22.14* 1	3.26 1	221.65* 1	15.14* 1	1.52 3	340	347
% T.L. in Tail/ lens diameter	F DF		257.78* 1				24.43* 1	.31 1	128	131
Axilla-groin/ lens diameter	F DF		251.31* 1				26.51* 1	.90 1	154	157
Snout-vent/ lens diameter	F DF		157.37* 1				7.61* 1	.07 1	154	157
Lens diameter/ total length	F DF		142.20* 1				7.90* 1	1.38 1	128	131
Span H. Legs/ lens diameter	F DF		20.28* 1				52.84* 1	6.95* 1	152	155

* Indicates significance

sigillatum and *columbianum*. Although the two latter races differ in several respects, band width is the most reliable diagnostic characteristic. Whereas the ratios indicate *macrodictylum*, *sigillatum* and *columbianum* to be strongly differentiated, *krausei* is apparently the least strongly differentiated, especially as compared to *columbianum*, to which it must be most closely related. Yet, the morphological resemblance between *krausei* and *macrodictylum* is greater than that between *krausei* and *columbianum*, inspite of the fact that the ranges of *krausei* and *macrodictylum* are completely disjunct with *columbianum* occupying the considerable intervening area.

Sex.—Sexual dimorphism has been demonstrated in 10 of the ratios tested and is apparently due to the following measurements in all cases:

Axilla-groin	Females > Males
Per cent total length in tail	Males > Females
Length of right front leg	Males > Females
Head width	Males > Females
Interorbital distance	Males > Females
Span of hind legs	Males > Females
Lens diameter	Males > Females

Interaction (sex x race).—Interaction proved significant for five ratios, all of which is attributable to a more pronounced sexual dimorphism in *macrodictylum* and *krausei* compared to *columbianum* and *sigillatum*. A similar situation was noted with respect to sexual dimorphism of the vent.

KEY TO ADULTS OF THE SUBSPECIES OF *A. MACRODICTYLOM*

1. Dorsal stripe interrupted on the body, forming irregular but sharp edged spots; or band edges deeply undulated; band pigment of the head in small distinct dots or flecks. 2
- 1A. Dorsal stripe continuous on the body, with parallel edges (may be absent, diffuse or indistinct in *macrodictylum*); band on the head continuous to the snout, broken into well-defined spots or appearing as diffuse flecks. 3
2. Band color dull orange (Raw Sienna); ground color jet black; Santa Cruz County, California. *A. m. croceum*
- 2B. Band yellow; ground color brownish black; head wide, combined vomerine count exceeding 33; Douglas, Klamath and Jackson Counties, Oregon and the Sierra Nevada of California. *A. m. sigillatum*
3. Dorsal stripe continuous onto the snout, usually expanded on the head between the eyes and with a large patch on each eyelid; edges of the stripe nearly parallel; combined vomerine count less than 34; Montana, Alberta and E. British Columbia. *A. m. krausei*
- 3C. Dorsal stripe broken into spots or flecks on the head and snout; pigment on eyelids variable; edges of stripe diffuse, slightly undulated or parallel; vomerine count variable. 4
4. Band pigment of head, snout and eyelids in diffuse flecks; band often nearly absent, dull in color and tending to blend into the ground color; white flecks on the lateral body surfaces numerous and coalesced; vomerine count less than 34; head short and narrow; lens of eye small; Wil-

- lamette Valley of Oregon and W. of Cascade Mountains in Washington and SW. British Columbia. *A. m. macrodactylum*
- 4d. Band on the head, snout and eyelids forming large distinct spots; band bright in color and abruptly demarcated from the surrounding ground color; white flecks on the lateral body surfaces separate; vomerine count exceeding 33; head longer and wider; lens large; Cascades of Oregon, Washington, and British Columbia, east to the Bitterroot Mountains of Idaho; north through central British Columbia to S. Alaska.
 *A. m. columbianum*

LIFE HISTORY AND ECOLOGY

Breeding.—*A. macrodactylum* migrates to breeding ponds at various times of the year in different parts of its range. The time of migration apparently depends largely upon climate. In the Willamette Valley of Oregon, males begin arriving at the ponds in late October or early November, the females arriving shortly thereafter. The actual movement seems to coincide with the onset of the fall rains. The breeding season in this area is greatly prolonged, and the animals may remain in the pond or nearby vicinity until around the middle of April after which they disperse. Such a dispersal was noted at a small pond about six miles east of Corvallis on April 14, 1955 (the day was warm following a week of heavy rain). Prior to this date, adults could be found only under boards, leaves and other debris at the water's edge. However, at this time none was found at the edge of the water, but thirty-three were collected from under logs and boards located from 15-300 feet from the water.

In contrast to the breeding pattern west of the Cascades where the species is apparently active all winter, excepting for brief cold spells, a definite winter hibernation period is evident east of the Cascades. In this region of very low winter temperatures and heavy snowfall, the adults arrive at the ponds much later. Ferguson (1954) reports gravid females and eggs being collected at La Grande, Oregon on April 6, 1954. The actual migration to the ponds probably coincides with the melting of snow and warming weather.

On Vancouver Island near Langford Station, 8 miles northwest of Victoria, Carl (1942) reports finding freshly spawned eggs on March 9, 1941. Fitch (1936) found freshly spawned eggs in mid-February and mid-March in the Rogue River Basin in Oregon. Bishop (1947) collected eggs and adults in ice-bordered ponds at Reflection Lakes on the slopes of Mt. Rainier, Washington on June 25, 1936. Kezer and Farner (1955) believed the eggs to be deposited in the vicinity of Crater Lake in May, June and July, depending upon the location and type of pond. Hatching eggs were reported at Mollman Lake (elevation 7,130 feet) in the Mission Mountains of Montana on August 3, 1950 by Brunson and Demaree (1951).

The total number of breeding individuals using a particular pond was found to be quite large by Storm and Pimentel (1954) who carried on marking and trapping studies near Corvallis, Oregon.

They report up to 394 individuals using a pond of one-seventh acre extent.

The number of eggs laid by the female is quite variable. Slater (1936) records taking 184 mature eggs from a female measuring 127 mm in total length. Below are listed the numbers found for several females from several localities in the present study. The date of collection indicates in a general way the breeding season for the area involved.

Locality	Total Length	Snout-Vent	No. Mature Eggs	Date Collected
Near Corvallis, Linn Co., Oregon	102.2	54.7	158	1/16/55
Corvallis, Benton Co., Oregon	133.0	68.0	199	1/1/54
Near Corvallis, Linn Co., Oregon	97.7	55.0	219	11/19/55
Near Corvallis, Linn Co., Oregon	107.3	60.7	208	11/19/55
Near Corvallis, Linn Co., Oregon	109.0	57.6	179	11/19/55
Near Corvallis, Linn Co., Oregon	104.5	58.0	130	11/19/55
Near Keno, Klamath Co., Oregon	132.0	70.5	345	4/4/56
Near Medford, Jackson Co., Oregon	105.6	58.6	198	3/20/55
La Grande, Union Co., Oregon	98.0	52.7	85	4/24/54
La Grande, Union Co., Oregon	-----	71.0	87	4/20/54
Moscow, Latah Co., Idaho	119.7	61.9	145	4/13/54

The eggs may be found singly but are more frequently in plinths, attached to the stem of an aquatic plant, rock or other object. Gravid females deposit masses of eggs on toweling when kept in the laboratory in large glass containers. A single mass may contain from 5-25 eggs but average 10-12 per mass. Slater (1936) described the ovum as 2.5 mm in diameter, black at the animal pole with the lower 2/5 at the vegetal pole being grey; two jelly envelopes are present with the line of demarcation between being indistinct; inner envelope 6-7 mm in diameter, outer 12-17 mm depending upon the age of the egg.

Larval Development.—Kezer and Farner (1955) found three rather clearly defined life history patterns for *A. macrodactylum* in the vicinity of Crater Lake: 1) One season larval period, where the

eggs are deposited in the spring, and the larvae transform in late August or early September. This appears to be the "normal" course of events. 2) Two season (or more) larval period wherein the larvae do not metamorphose the first year but over-winter and do so the following year, attaining a length of 70-90 mm at the time of transformation. 3) Facultative one season larval period wherein the larvae are forced to metamorphose by the drying of a semipermanent pond. These larvae form very tiny transformed individuals.

Similar patterns are probably found throughout the ranges of *sigillatum*, *columbianum* and *krausei*, the type of pond and elevation determining the one present in a given area, with seasonal variations caused by macroclimate. Evidence is lacking that *A. m. macrodactylum* ever has a two-year larval period. Young *krausei* from Kootenai Crossing, British Columbia examined by me fall into two definite size classes, representing some animals of the two-year larval type (large gill scars, a faint band and a line or seam present down the dorsal midline representing the vestiges of the tail fin) and some which metamorphosed the first year (small, adult pattern and no gill scars evident). Recently metamorphosed *columbianum* from several localities in Deschutes County, Oregon appear to belong to the two-year larval class. Stebbins (1951) mentions larvae of two distinct sizes reported by H. J. Snook in Alpine County, California. Dr. James D. Anderson (personal communication) reports all three life history patterns in Sierra Nevada populations, but states that the distinction between 1 and 3 (above) is not always clear.

Dr. R. B. Brunson of Montana State University (personal communication) has called to my attention the very small size of newly metamorphosed young in western Montana, where the facultative pattern is apparently common. The smallest metamorphosed individual examined was from that area.

Habitat.—Ecologically and geographically, *Ambystoma macrodactylum* is one of the most adaptable and variable salamanders in the Northwest, surpassing all other species in these respects. Confirmation of this fact is evident in the range of the species, which includes sagebrush semi-desert and all the intermediate vegetative types up to alpine meadows.

In the Willamette Valley *macrodactylum* is found in bottom land situations or in oak woodlands along the valley edges, where it breeds in permanent and semi-permanent ponds. Although the animal is easily found near such ponds during the breeding season, it is exceedingly difficult to locate at other times. It apparently leads a subterranean existence during the dry season, probably residing in rodent burrows and other underground excavations. Although it is repeatedly depicted as being found on the Oregon coast, the species does not appear to occur in the coastal type forests surrounding the valley. Moreover, only two records are available from the coast, one on the Rogue River and Baird's record from near Astoria, both of

which are located on large rivers draining inland areas where the animal commonly occurs. It is questionable whether the species inhabits other coastal areas not drained by large streams transecting the Oregon Coast Ranges.

Of the four subspecies treated here, *columbianum* is probably least restricted as to habitat distribution. It has been recorded from 7,800 feet (Hudsonian Life Zone) in the Wallowa Mountains of northeastern Oregon (Ferguson, 1952b) where the vegetation consists of stunted willow (*Salix sp.*), limber pine (*Pinus flexilis*), and various grasses and sedges. Less than 40 miles from this locality, the animal has been found occupying an abandoned mine shaft at a place about 10.3 miles north of Home in the Snake River Canyon of Baker Co., Oregon by Ferguson, *et al.* (1958). This locality is Upper Sonoran Life Zone (elevation roughly 1,800 feet), the vegetation being primarily a sparse cover of sagebrush (*Artemisia tridentata*), cheat grass (*Bromus tectorum*) and scattered hackberry trees (*Celtis douglasii*). Ferguson (1952a) reported adults being difficult to locate during the summer but larvae abundant in springs and ponds throughout the yellow pine forested areas of Wallowa County, Oregon.

Fitch (1936) found *sigillatum* to occur irrespective of life zone from Crater Lake down to less than 2,000 feet in the Rogue River Valley, a fact further indicated in the present study by collections made near Medford (1,150 feet) and Crater Lake (6,170 feet). Fitch believed the adults to be subterranean in habit during the dry seasons in the Rogue River Valley. However, at Crater Lake, Farnier and Kezer (1953) were able to obtain adults throughout the summer along the edge of the lake. Stebbins (1951) mentions records from 6,820 and 7,000 feet elevation in Alpine County, California. Also, Anderson (personal communication) has found them a few feet shy of 9,000 feet in Alpine County.

A wide variety of habitats and elevations are also occupied by *krausei*. Brunson and Demaree (1951) report it at 7,130 feet in the Mission Mountains. Several records are available from the Bitterroot Valley near Missoula. Specimens of *krausei* were obtained July 15, 1955 near John's Lake, Glacier National Park, Montana (elev. ca. 3,500 ft.) from an unusual habitat. In working around the lake, although all likely looking logs, sticks and other objects were turned and a thorough search made for salamanders, only a single recently metamorphosed animal was found. However, just before giving up, a fallen log was torn open and a salamander was found. Continued search yielded five other animals in rotting hemlock (*Tsuga heterophylla*) logs, most of which were located 25-100 yards from the water. The lake is surrounded by a rather dense forest of spruce (*Picea engelmanni*), western red cedar (*Thuja plicata*), hemlock and scattered maple (*Acer sp.*), resembling the type of forest found in parts of western Oregon. The niche was similar to that occupied by the salamander *Aneides ferreus* in western Oregon, where it fre-

quently occurs abundantly in rotting Douglas fir logs (*Pseudotsuga menziesii*).

Russell and Anderson (1956) described the habitat of *croceum* in considerable detail. Briefly it is predominantly oak forest (*Quercus agrifolia*), with Madrone (*Arbutus menziesii*) and Douglas fir (*Pseudotsuga menziesii*) sparingly represented.

When *columbianum* from Union Co., Ore., *sigillatum* from Jackson Co., Ore. and *macrodactylum* from Benton Co., Ore. were placed in finger bowls with moist toweling, the *macrodactylum* sought refuge beneath the toweling, the others being content to remain exposed. This was interpreted to indicate a lesser ability in *macrodactylum* to cope with drying. Preliminary dehydration tests, in which *macrodactylum* lost an average of 33.5 per cent of their original body weight compared to 28 per cent loss in *columbianum*, appeared to substantiate the hypothesis. However, small samples were used and the studies were discontinued when additional living specimens could not be obtained simultaneously from the two areas due to seasonal variation in availability.

Notes on Food, Enemies and Size.—Detailed studies were not made of food habits, this aspect having been investigated by Farner (1947) and Schonberger (1945) at Crater Lake. Their work indicates the species to be primarily scavengers, feeding largely on insects and insect parts. Farner found *A. m. sigillatum* not to feed on snails, whereas *Taricha*, which frequently occurred under the same rock, did do so. However, in the present study, two types of snail shells were abundant in the fecal pellets of several *A. m. krausei* from Eisenhower Forks, Alberta, Canada.

Regarding enemies, adults probably do not often fall prey, they being so secretive at times other than the breeding season. However, two adults in the University of California Collection (MVZ 24707 and 24698) were removed from the gut of a garter snake (*Thamnophis*) collected in Creighton Valley, British Columbia. Larvae are probably devoured in quantity by predaceous aquatic insects and garter snakes. On April 10, 1956 near Corvallis, Oregon two *Thamnophis sirtalis concinnus* were observed actively foraging in a shallow pond containing large numbers of *A. macrodactylum* larvae.

The largest *A. macrodactylum* examined was a female *columbianum* in the College of Puget Sound Collection (CPS 3011) from 21.3 mi. NE Goldendale, Klickitat Co., Washington. Measurements (after preservation) were 155.6 mm in total length (167 mm in life) and 79.6 mm snout-vent. This exceeds the largest previously known specimen from Wallowa Co., Oregon which measured 155 mm before preservation (Ferguson, 1952b). A preserved male from near Philomath, Benton Co., Oregon measured 151.3 mm in total length and 74.0 mm snout-vent. Two specimens from Plumas Co., California approach these maximum figures.

The smallest transformed animal examined was a specimen from John's Lake, Glacier National Park, Montana (DEF 606, now in the Park Collection), which measured 43 mm in total length and 29 mm snout-vent.

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Social Behavior of the Desert Pupfish, *Cyprinodon macularius*, in the Field and in the Aquarium

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ABSTRACT: A glossary of the motor patterns of the desert pupfish is given. Reproductive, territorial and group behavior is analyzed in detail. During the breeding season the female visits the territorial male; rarely, males leave their territories and pursue the females in order to spawn with them. When approached by the male, the female nips the bottom, the male sidles against her, she halts and forms an S-shape, the male S-shapes along side the female and wraps his anal fin around her vent, she jerks releasing an egg, the male jerks fertilizing the egg, and the pair separates.

In a fully developed fight two males approach head on, turn away slightly and stand momentarily eye to eye, advance and arch, give tail-beats, charge at one another, and finally circle head to tail rapidly around one another before separating.

During the spawning season males hold territories, and these sometimes contain sub-territories along the periphery which are held by smaller males. Females were never seen to hold territories under natural conditions.

Female and juvenile pupfish move about in schools and forage in groups. In the cold season the males join the schools.

INTRODUCTION

The interpretation of animal phylogeny through the comparative study of species-specific behavior patterns started with the independent works of Whitman (1899, 1919) and Heinroth (1911). It was not until the recent writings of Lorenz (1939 in Schiller, 1957) and of Tinbergen (1940, 1951) that this approach to the study of behavior gained impetus. So far the rewards have been exciting but limited; in most animal groups the total body of information is still too small (see review by Eibl-Eibesfeldt and Kramer, 1958).

An excellent example of a numerous and well known group of animals whose ethology is virtually unknown are the teleost fishes of the family Cyprinodontidae, the toothcarps. A brief ethogram of the breeding behavior of *Oryzias latipes* (Temminck and Schlegel) has been published by Ono and Uematsu (1957), and a short account of the behavior of *Fundulus notatus* (Rafinesque) has been given by Carranza and Winn (1954), and that of *Fundulus diaphanus* (Le Sueur) by Richardson (1939); Koster (1948) has published a note on the spawning activities of a closely related species, *Plancterus kansae* (Garman). Peters (1941) has presented a condensed description of the social behavior of *Jordanella floridae* Goode and Bean. Newman (1907), and Raney *et al.* (1953), have reported on some aspects of the behavior of *Cyprinodon variegatus* Lacépède. The article by Raney *et al.* (1953) also cites incidental observations from

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the literature on different species of *Cyprinodon*. Within recent years aquarists have photographed the behavior of fishes with the aid of electronic flash equipment; the articles in various aquarium journals by Foersch in particular are of use in the comparative study of tooth-carpers because of the excellent photographs.

It is the purpose of this paper to describe the motor patterns and social behavior of the desert pupfish, *Cyprinodon macularius* Baird and Girard. The reader should appreciate that this short paper can only be an introduction to the ethology of the desert pupfish.

I am indebted to Donald K. Adams, Boyd W. Walker, and Wolfgang Wickler for critically reading the manuscript. Thanks are also due to John Wintersteen for filming the spawning behavior of the desert pupfish and to Herman Kacher for preparing the illustrations. Clark Hubbs kindly made available certain of his field notes on the behavior of other species of *Cyprinodon*.

MATERIALS AND METHODS

Adults of both sexes of the pupfish often attain a standard length of 45 mm. One exceptionally large female 72 mm in length was collected. Sexual maturity may occur in males as small as 15 mm long, and the same probably holds for females.

When mature the sexes are distinctly dimorphic and dichromatic. The body shape of the male is compressed and arched at the nape, whereas the shape of the female is rounded (Fig. 1A). In the breeding season the body, and the dorsal and anal fins of the male are dark metallic blue; the caudal peduncle, caudal fin, and pectoral fins are yellow-orange. The eyes are black, and so are the posterior margins of the dorsal and anal fins. The lower distal portions of the pectoral fins are much darker than the other parts of the fins. When the water is clear these males can be seen at distances up to 10 meters. The head and body of the female are yellowish brown with irregular darker brown blotches; the fins are similarly colored. During the spawning act the body is paler and an interrupted brown line extending mid-laterally the length of the body becomes more apparent. Except for the small dark ocellus found at the posterior base of the dorsal fin in the female, the juvenile and female markings are the same. The colors of the female and of the juvenile pupfish render the fish inconspicuous because they correspond to those of the algal mats which coat the bottoms of the desert pools that are their habitat.

The desert pupfish is widely distributed in the desert springs and drainages of the lower part of the Colorado River Basin (Miller, 1943). In the Salton Sea the pupfish occurs in shallow shore pools where they are easily observed. This habitat, and some aspects of the ecology of the pupfish therein, have been described elsewhere (Cowles, 1934; Barlow, 1958). More general information on the ecology and life history of the desert pupfish can be found in Miller (1943, 1949).

Almost all of the observations from the field were on pupfish living in shore pools along the Salton Sea. Supplemental observations were made at nearby Fish Springs. The shore pools were visited at about monthly intervals over a two year period from 1954 to 1956. Most observations were made in the forenoon although the fish were also watched at other times of the day as well as during the night.

Pupfish of mixed sexes and sizes were also maintained in a freshwater aquarium, having a capacity of 68 liters, which was well planted. Previously isolated males and females were put together in 45 liter aquaria which contained no plants; the bottoms were covered with fine gravel. This experiment was repeated four times, and in each instance the female was the resident fish. An additional pairing was filmed in color at normal and at high speeds. The film proved especially useful in the descriptions of the motor patterns.

MOTOR PATTERNS

The characteristic movements which constitute the behavioral repertory of the pupfish have been given names to facilitate discussion. Convenience has been the rule in deciding which complex of motor patterns should be considered as units. Thus *patrolling*, which actually consists of several motor patterns, is treated as one element. The individual movements, however, are described. On the other hand, *wrapping* seems to represent a single motor pattern, and it is described as another unit in the behavior on a par with *patrolling*.

Meandering.—The female swims slowly in midwater or near the surface, changing course frequently and rather aimlessly. Swimming movements seem to be slightly exaggerated. The median fins are held against the body.

Nuzzling.—The male swims directly under the female while she meanders. His body is tilted up about 30° , and he maintains a position in which the top of his head is just below, or in contact with, the abdominal region of the female (Fig. 1D). (The abdominal region here includes the ventral surface from directly below the pectoral fins to just posterior to the vent.) The median fins of the male are folded.

Contacting.—As the female moves slowly over the bottom the male stays beside her, and her head is usually just in front of his. Often they are actually touching. In the early stages of the mating the male usually contacts the female anteriorly in the region of her pectoral fin base with his snout. As mating proceeds, the male contacts the female progressively more posteriorly. Eventually, the area of contact is almost restricted to the region of the vent. During most of this time the dorsal fin is folded. Movements of the male which are directed at keeping station beside the female are called *contacting*. Side to side contacts are not separated from snout to side contacts.

Tilting.—While swimming slowly over the bottom the female tilts her body toward the bottom, head down, at an angle of about

45°. The dorsal fin is normally raised at this time. Tilting is the beginning movement of nipping.

Nipping.—From the tilted position, the female opens her mouth, presses it against the bottom, and normally takes up a mouthful of the substrate (Fig. 1B). Then the body is dropped down against the bottom. When horizontal, the female either immediately spits out the substrate, or swims forward a short distance, stops, and then expels it. The female appears to turn the substrate over in her mouth. The dorsal fin is held open. The female may nip two or three times in quick succession; each successive nip after the first one is initiated from the horizontal position. Females of another toothcarp, *Cyprinodon variegatus*, were seen by Raney *et al.* (1953) to pick up objects from the bottom when encountered by males, and this action was interpreted as food-seeking. In the roach, *Leuciscus rutilus* (L.), and in the goldfish, *Carassius auratus* (L.), the female evidently signals the moment of spawning by snapping at some object as if feeding (Fabricius, 1959).

Halting.—The female stops swimming after nipping. Usually her vent is close to the substrate so that the long axis of the body is tilted up slightly anteriorly (the male assumes a corresponding angle). The dorsal fin is still spread.

Sidling.—The male swims forward and laterally against the female. The male's dorsal fin is folded or half open. The region supporting the anal fin of the male is thrust against the posterior line of the abdomen of the female. The body of the male is tipped out of the median plane only slightly, or not at all. In this maneuver the male cannot swim by means of trunk undulations and must therefore rely on sculling movements of the free pectoral fins and of the caudal fin. This rapid sculling imparts a quivering appearance to the male.

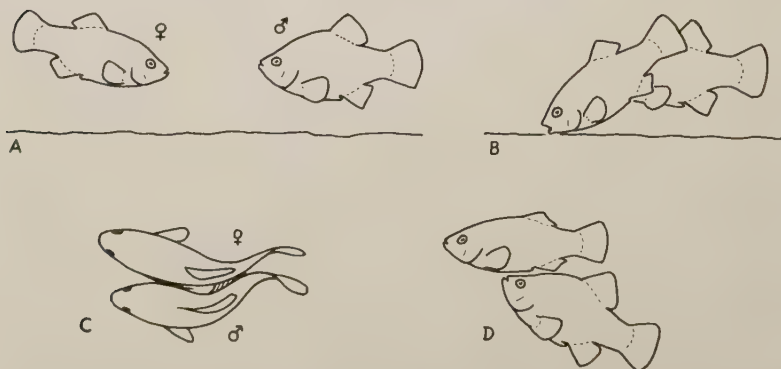


Fig. 1.—Motor patterns of the desert pupfish. A. A male approaching a female. Note the rounder profile of the male. B. The female just about to nip while being contacted by the male. C. The male and female S-shaping; the male is also wrapping. D. The male, below, nuzzles a meandering female.

S-shaping.—Seen from above, the body of the pupfish forms a gentle "S" (Fig. 1C). At this time the male and female normally lie side by side on the bottom in parallel S-shapes. The curvature is more pronounced in the male. The head and the anal region of the male are directed toward the female, and the anal fin of the male is extended in her direction. The dorsal fin of the male is spread, and sometimes is bent slightly toward the female. In the female the dorsal fin is spread maximally. Moreover, her vent is pressed against the bottom and her caudal fin beats rapidly, but with a very small amplitude.

Wrapping.—While both fish are S-shaped the male wraps his anal fin around the posterior line of the female's belly (Fig. 1C). The male's anal fin forms a crude cup under the vent of the female. The extended dorsal fin was sometimes bent toward the female, but it was never seen to enfold her.

Jerking.—While still S-shaped the head is jerked toward the side opposite that to which it is already directed, thus initiating a wave of contraction which passes down the body reversing the direction of the S-shape. In the female one egg is extruded by this flexure, and the male presumably emits sperm at this moment.

Patrolling.—The male in his territory swims straight ahead in spurts of about 30 to 50 cm with the dorsal, anal and pectoral fins folded back. The lateral beats of the orange caudal fin contrast against the bright blue body. At the end of each spurt the male stops abruptly by throwing the colorful pectoral fins forward together in a quick movement that catches the eye. Then the male stands momentarily with the median fins raised, and the pectoral fins beating alternately and rapidly. The caudal peduncle is frequently flexed to one side in the intention swim posture. Then he swims off again in a new direction. In this manner the male pupfish continually crisscrosses his territory.

Facing.—Males approach one another head on and usually pause momentarily face to face about one body length apart. The median fins are spread.

Eyeing.—Two male stand momentarily eye to eye facing in opposite directions, bodies parallel, and about one half body length separating them. The median fins are spread.

Arching.—The body is bent into a C-shape with the concave side toward the other fish. The median fins are spread. A sculling action of the caudal fin and the pectoral fin on the convex side imparts a slight quivering appearance to the fish.

Tail-beating.—The flexure of the peduncle appears to be reversed from the arched position so that the caudal fin, apparently folded, is first directed away from the other fish. Then the spread caudal fin is beaten back toward the opponent, often causing the

head of the fish delivering the beat to swing away. This movement requires further observation.

Charging.—The median fins are folded, the mouth is opened, and the fish darts forward toward another fish.

Circling.—From the arched position two fish often start to circle at high speed while maintaining the head to tail orientation. It seems that each fish attempts simultaneously to charge into the flank of the other and to dodge the charge of the opponent by turning.

Fleeing.—The fish swims away from the attacking fish at high speed with the median fins folded. Flight is toward the surface in the absence of cover, but if plants are present the fish will sometimes take refuge among them.

Escaping.—The fish darts toward the bottom and into the mulch, algae, or plants there, and then lies motionless. Cowles (1934) observed this behavior in free living pupfish which he tried to capture.

Digging.—While standing over the bottom, with head and body tilted downward about 45° , the fish moves ahead, *i.e.*, obliquely downward while opening the mouth. The mouth contacts the bottom; substrate is taken into the mouth; the fish rebounds; the body is tilted up into the normal horizontal position as the fish moves forward slightly; and the substrate is expelled through the mouth. The substrate is often expelled immediately at the end of the rebound.

Plowing.—This movement starts just like digging, but when the substrate is taken into the mouth, the fish then drops the body down against the bottom and swims forward through vigorous beating of the tail. At the same time, the pectoral fins beat forward resisting the thrust of the caudal fin. The fish briefly swims in place expelling bottom material both forward and backward. Then the pectoral fins cease to resist the tail propulsion, and the fish moves forward expelling the mouthful of substrate. After this the pupfish commonly returns to the excavated spot and digs there in the normal manner. According to the description by Raney *et al.* (1953), *Cyprinodon variegatus* plows in the same way. Plowing in *Cyprinodon* seems similar to the movements in cichlid fishes which have been called digging by Baerends and Baerends-van Roon (1950).

REPRODUCTIVE BEHAVIOR

The behavioral acts in the reproduction of the pupfish proceed in a characteristic sequence. The sequence of events described in the following represents a composite of four series of observations on different pairs of pupfish in aquaria.

When a male is introduced into the aquarium he sinks to the bottom where he remains motionless. His colors fade slightly, apparently due to the handling. The female immediately fixes on the male and moves toward him. This is followed by aggressive behavior by the female. She starts by arching while facing the male.

The tail of the female is brought around and directed toward the male. Then she backs in the direction of the male while maintaining the arched position. When her tail is near the head of the male she commences tail-beating. The blows are directed at the head of the male. The male responds by fleeing, normally toward the surface, or less often by arching and returning tail-beats. In the latter case the two fish may charge at one another leading into circling head to tail. This is typical fighting as seen between two males.

The aggressive activity of the female is sporadic. After a variable period both fish become inactive, and the colors of the male return. They lie on the bottom about two to three body lengths apart and facing one another. The attention of the female is fixed on the male. Five to twenty minutes after his introduction into the aquarium the female suddenly nips the bottom. At once the male swims to her side and contacts her. She swims forward over the bottom with the male maintaining contact. The female tilts about every 3 to 5 seconds, and some of these movements develop into complete nipping. The male drops back slightly after each nip by the female and attempts to sidle. At first this seldom develops into wrapping because the female does not halt completely. Each nip-to-sidle sequence brings the pair a little closer to complete spawning. At about the third to fifth nip by the female the male usually succeeds in wrapping because the female now halts completely. Sidling by the male apparently releases S-shaping by the female, which in turn causes the male to S-shape, and almost concurrently, to wrap the anal fin around the vent of the female. Wrapping then releases jerking in the female, which is almost simultaneously followed by jerking in the male. The pair separate and one egg is left on the bottom. Rarely, the female immediately S-shapes and the sequence proceeds through to jerking again without the pair separating. Successive jerks indicate that up to five eggs may be spawned in quick succession. Normally the pair moves forward a short distance between successive jerks. Sometimes when they separate the female swims up into midwater and meanders. The male accompanies her and continuously nuzzles her.

The spawning lasts from 30 minutes to 2 hours, larger females spawning longer than smaller. Usually the last union of the pair is the most prolonged, and several eggs are released in quick succession, then both fish lie still on the bottom. After about 2 seconds the male starts contacting the female again. If the female is through with spawning she darts toward the surface. The male pursues and the female seems "panicky," sometimes breaking the surface. This rapid and evasive swimming by the female contrasts sharply to meandering. After about 5 minutes the male stops chasing the female. Both swim to the bottom and without further interaction start foraging.

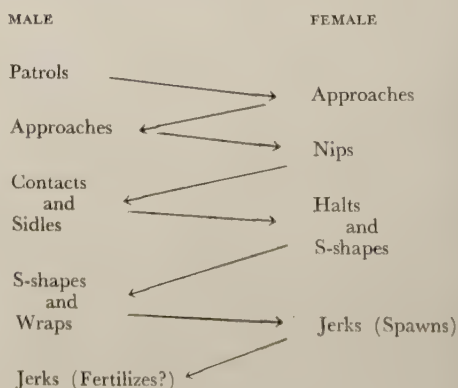
Most of the variations observed could be considered under one or the other of two categories. The first is orientation. In the initial

stages of spawning one male contacted the female at first in the region of the pectoral fin, and later only near the vent; another male contacted first and only near the vent. Abortive contact resulted when a male once contacted a female who was about 5 cm over the bottom of the aquarium. Later this male attempted, without success, to contact the female while facing the opposite direction, i.e., situated head to tail. One female oriented her spawning activities to the bottom in the normal fashion during the first half hour of spawning, but in the next 20 minutes she oriented to one glass wall as though it were the bottom. She stayed parallel and adjacent to the water surface with her ventral surface against the glass wall. She nipped the glass though no gravel was present. The male did not contact until the female assumed the S-shape. Then the male oriented to the female, not the substrate, and the pair spawned.

Another source of variation lies in the sequence of movements. This type of variation is most obvious at the beginning of pairing. Usually one fish appears at first more inclined to spawn than the other. For example, one female invited the male to spawn by nipping, but when the male contacted her, she responded by arching and tail-beating. During 3 to 4 more contacts by the male the behavior of the female gradually became synchronized with that of the male, and spawning proceeded following the typical sequence.

Even when the pair finally is synchronized the sequences varies, but the variation is not random. In the behavioral sequence shown by the male from approaching to wrapping, for instance, if the female is not ready to halt, the male may stop sidling or wrapping and revert to contacting. Where he starts again depends on the behavior of the female. If she moves away the male may revert to contacting. But if the female resumes S-shaping, then the male also starts at S-shaping. Thus elements in the sequence also may be omitted. At the peak of spawning, about one out of every four contacts proceeds to jerking. Ultimately the variation in sequence is due to the variation in the physiology of the two fish. For example, a female whose threshold for releasing an egg is presumed to be low, stays in place when she nips, but when the threshold is presumably somewhat higher, she moves forward as much as two body lengths before halting. At an apparently higher threshold she may tilt without nipping. And this determines the response by the male.

The sequential nature of the reproductive reaction chain is given in the



style of Tinbergen (1942). This diagram applies to naturally occurring populations, not to pupfish in aquaria, and represents an "ideal" stimulus-response chain.

Some elements of the behavior of the pupfish seen in aquaria were lacking or uncommon in the natural population. No female was seen to meander although once a male was observed nuzzling a female which was lying just under the water surface. Contacting infrequently was seen as a behavioral unit separate from sidling.

Two different types of reproductive behavior were observed in the field. In the typical situation the male remains in his territory and the females, alone or in groups, visit him there. If the female is alone it is almost certain that a spawning will occur at once. Usually only one egg is laid, they separate, and the female swims away. If a group of females enters the territory, the male swims directly to the nearest one and pauses. He swims from one female to the next until one gives the proper response. The females without eggs forage continuously. When the male encounters a female who is ready to spawn, she nips, the male immediately sidles, and the sequence runs through to jerking. Then they separate, the male resumes patrolling, and the females move on, alternately schooling and foraging. Rarely the male from a neighboring territory rushes to the side of the female opposite the first male, and spawns with the pair. Raney *et al.* (1953) reported that in *Cyprinodon variegatus* two males sometimes spawn together with one female.

A kind of reproductive behavior seen less frequently occurs when 1 to 3 males pursue a given female over considerable distances without regard to territorial boundaries. The female does not meander, but swims rapidly. Every 1 to 3 meters the fish stop on the bottom and spawn. On one occasion a group of 3 males and 1 female remained still on the bottom for about 4 seconds after spawning. The spawning groups never stopped in the occupied territory of another male. I was unable to determine whether or not males spawning outside territories themselves held territories. *Cyprinodon variegatus* also shows both of these types of reproductive behavior (Raney *et al.*, 1953).

Two chance observations are worth noting because of their relevance to the problem of sex recognition in pupfish. A group of males were held together in a small tank with a capacity of about 30 liters. One large male quickly became dominant. He continuously pursued the smaller males. Finally one fish was so exhausted by the dominant male that it could no longer flee. Then the large male sidled against the smaller, S-shaped, wrapped, and jerked. This behavior was repeated many times within an hour. On another occasion 3 previously isolated females were placed in a beaker. About one-half hour later a brightly colored male was put into the same beaker. The male sank to the glass bottom, faded slightly, and remained motionless. One of the females swam directly to him, pressed herself against him, S-shaped, and jerked. The male did not respond.

AGGRESSIVE BEHAVIOR

The size of the opponent appears to determine the first response of a territorial male. If the other pupfish is a smaller male (but not too small, see p. 352), usually the first move of the larger fish is to charge straight at the opponent, who generally flees. If the opponent is at least as large, or larger, the two commonly face one another, and then in rapid sequence eye one another, arch, give tail-beats, and finally charge and circle. At this point the fight normally breaks off. If one flees, the other may pursue. Evenly matched males commonly swim away from one another after circling; however, they may stand about one body length apart, arch, and give emphatic tail-beats. This can lead into charging and circling again.

Fighting can be observed among both male and female *C. macularius* throughout the year in a well-lighted and warm aquarium. Males, however, fight more than females. The fighting in females is rarely carried to circling. In addition, males attack females when the males are not ready to spawn, as Cowles (1934) has noted.

Fighting among pupfish in the desert pools is similar to that observed in aquaria. Noteworthy variations and comparisons, such as whether or not a male attacks females, or smaller males, will be considered in the description of territoriality.

TERRITORIALITY

The males of different species of *Cyprinodon* are well known for their pugnacious defense of territories (Newman, 1907; Cowley, 1934; Raney *et al.*, 1953). When placed in a new aquarium, males of *C. macularius* fight considerably until territorial boundaries are established. After this the amount of fighting is reduced and restricted to the boundaries; each male stops there, arches as the neighboring male approaches and then each swims back toward the center of his territory. Rarely one charges at the other and then both circle quickly and depart. Intruders that stray into a territory, at first unnoticed by the resident, elicit a head-on charge by the latter when he finally discovers them. The intruder almost always flees. Fish without territories flee into thickets of plants, or toward the surface.

Due to the spatial limitations imposed by the aquaria, the territories established in them were comparable in size only to the smallest seen in natural pools. The maximum number of territory holding males in a tank with a bottom measuring 30 cm by 60 cm was 4, varying in standard length from 25 mm to 30 mm. Moreover, it is almost impossible to induce only 2 males to maintain territories in the same aquarium. Invariably one supplants the other and dominates the entire bottom.

The presence of food determines the territorial center of the largest male. It is possible to shift the territory of the largest male as desired by gradually changing the place where the food is put into the aquarium.

Females defend territories only when the number of fish in the tank is small, and this behavior is rather sporadic. But when aggressive, females will sometimes defend territories in aquaria even against smaller males. Where several females are together the larger and stronger ones defend the center of the feeding area at feeding time. Otherwise a rank order is maintained, though this has not been observed in detail.

Male pupfish in the shore pools defend certain areas during much of the year. The consistent holding of territories extends from mid-April, or May, to October. During periods of warm sunny weather in the winter males sometimes come into nuptial coloration and take up territories, as was observed on 11 February 1956. The females were never seen to hold territories. However, Raney *et al.* (1953) reported one instance of a female *Cyprinodon variegatus* briefly maintaining a territory in a pool against other females.

The holding of territories in the pools seems to fluctuate during the day, but this requires further observations. Large males were seen now and then to leave their territories late in the afternoon to forage in shallower regions of the pools although they forage within their territories as well. Raney *et al.* (1953) noted that *C. variegatus* males also stray from their territories. At night most territorial males of *C. macularius* sleep in their territories, whereas the non-territorial pupfish sleep in the shallowest possible water. At sunrise territorial and non-territorial fish alike congregate in the deepest parts of the pools (Barlow, 1958).

Male pupfish maintain territories in different parts of the pools, and certain features seem to characterize these territories. First, they are never located in deeper (one meter) parts of the pools. A typical situation is one where territories are located in water about 5 to 10 cm deep and along the edge of a drop-off into deeper water. Secondly, marked irregularities in the topography of the bottom are usually present. Territories are centered about such objects as submerged bushes, pieces of wood lying on the bottom, corners or coves along the shore, or outstanding features of the bottom profile. This is especially clear where large areas of the bottom are flat. There, at the peak of the breeding season, nearly every piece of debris is patrolled by a brightly colored male.

The male pupfish recognizes his territory by several features of the terrain. One male was seen patrolling up and down a sunken palm frond. The frond, about one meter long, lay flat on the bottom, half in and half out of a tiny cove, and extended away from the shore at a right angle. The cove was semicircular in shape with a radius of about 50 cm. The territory of the male included the cove and extended out into the pool along the frond. I moved the frond so that only one third of its length remained in the cove. The male returned to the cove shortly, swam to the frond, and resumed patrolling along it. Then I moved the frond so that it lay just outside of the cove. Again the male returned first to the cove, but then patrolled along

the frond. Finally, I moved the frond about one meter away from the cove (for each move the water depth remained approximately the same). As before, the male went to the cove and from there to the frond. However, after the male swam up and down the frond once, he returned to the cove and thereafter patrolled only in the cove. Apparently the cove was ultimately more attractive than the frond in open water.

The size of each territory varies according to the influence of several different factors which are not well understood. It is clear that larger males hold proportionally larger territories than the smaller ones. From general observations it is also apparent that territories are small when the population density is high, and large when the population density is low. On the other hand territories may be large in the midst of the breeding season when pupfish are numerous. This seems to result from a disinclination of most of the males to fight for territories during those periods. The few aggressive males dominate large areas with little need to defend them. For instance, on 4 June 1955, individual territories reached the relatively enormous sizes of 5 to 6 square meters as compared to the customary size of about 1

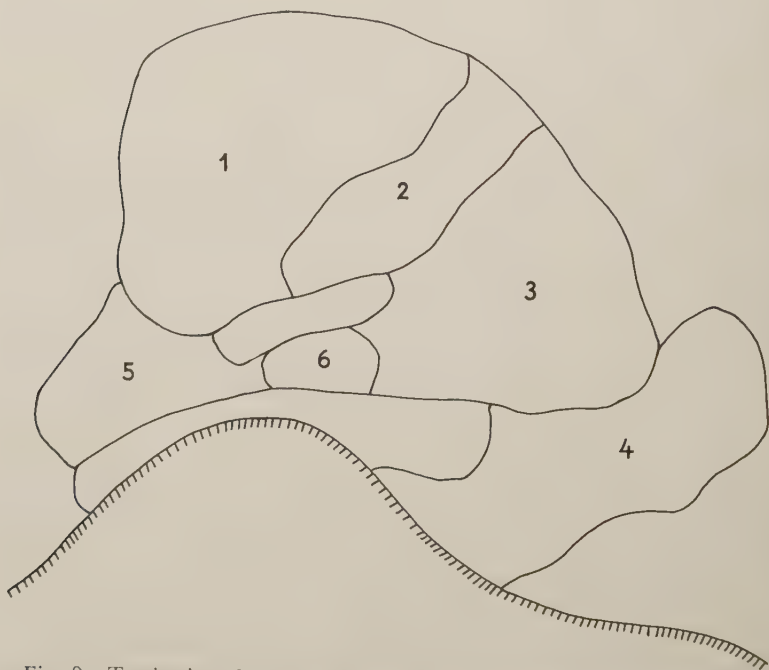


Fig. 2—Territories of six male pupfish. At the bottom of the sketch is the shore line. The enclosed area adjacent to the shore represents a patch of sand, approximately 1.4 m wide; the numbered subdivisions portray the territories, whereas the unnumbered subdivisions show the neutral areas.

to 2 square meters. The males were not particularly aggressive and chased intruders without the customary vigor. The intruders fled immediately. No spawning was seen, and one male forsook his territory during the hour of observation.

High temperatures also play a role in the regulation of territory size. On the afternoon of 5 August 1956, observations were made on a small (5 by 10 meters), densely populated pool (approximately 150 pupfish per square meter) with an almost uniform water temperature of 38.3°C. In larger pools pupfish can and do avoid temperatures over 36°C. to 37°C. (Barlow, 1958). It appeared that every member of the population of this pool was actively foraging. Most of the bottom was thickly carpeted with blue-green algae, but along the shore there was a patch of free sand about one and one-half square meters in area. The small sand patch contained territories of six different males (Fig. 2). Although the males did not actively patrol, their occasional forays indicated the boundaries of the territories and of the two neutral areas. Each male tended to stay in the center of his territory and plow and dig for food almost continuously. Three males with the smallest territories (number two, five, and six) tolerated females some of the time, and displayed by arching before attacking intruders. At different times the territory of male number six contained from 5 to 15 females. The males with small territories spent most of their time foraging, often responding to an intruding fish by merely raising the median fins without stopping foraging. The three males with the largest territories (one, three, and four) defended them vigorously; all intruders were driven out by a straight ahead charge. Once territory number four was overrun by about 40 females. The male holding this territory attacked them vigorously and it took him approximately 5 minutes to drive them out. Meanwhile yet another male next to the sandy region was defending an algal-coated area almost as large as the entire sand patch. He was constantly occupied with preventing the encroachment upon his territory by the many females and smaller males and thus was unable to search for food. At the high temperature of 38°C. it seems that pupfish are almost compelled by metabolic demands to seek food continuously. The time and effort expended by males in defending such large territories must handicap them in the competition for available energy. [*i.e.*, food.]

Apparently there was a constant threat of encroachment on the territories by the non-territorial pupfish. Yet male number one left his territory and stayed away for more than thirty minutes, during which time only one other fish entered this territory. Males number two and five observed the boundaries between their territories and that of male number one as though the latter were still present. Rarely male number two crossed the boundary, but quickly turned back. A new and smaller male entered the unoccupied territory after first foraging along its shoreward edge. After about 5 minutes the small male moved to the center of the territory and began returning

the displays of neighboring males. Then the small male deserted the territory, apparently without being driven off. The territory remained unoccupied.

The small sizes of the territories limited the activities of the males to such a degree that they tended to dig and plow in one spot only. Most of this excavating was done by plowing. The most interesting and rarely seen consequence was that small pits were built. Male number one made one pit and male number six excavated three adjacent depressions. Each pit had a raised lip and was about 2.5 cm deep and 6.5 cm in diameter. Nearby males whose territories were carpeted by blue-green algae were unable to dig pits. Since the bottoms of most of the shore pools of the Salton Sea are covered with algae it is not surprising that pupfish were never observed excavating pits at any other time.

Most male pupfish are the sole possessors of their territories. Not infrequently, however, constellations of smaller males are seen holding territories within that of a larger male. Observations made at 1700, 14 May 1955, are cited as one example. The territory of a large (45 mm long) male measured about 70 cm by 50 cm. The four smaller males which shared the territory ranged in length from about 20 mm to 25 mm. The boundaries of the subterritories were not distinct although the centers of activities of the small males were obviously within the territorial boundaries of the large pupfish. All five males drove off intruders, but not jointly. And the larger male drove off in turn each of the smaller males. The latter always fled after briefly circling with the larger pupfish. Then the dominant male resumed patrolling and within 2 to 3 runs across the main territory encountered and drove off another small male. By this time, however, the first small male had returned. The procedure repeated itself each time the dominant male encountered one of the smaller males. On most other occasions large males were seen to attack even smaller males (about 15 mm in length) that were already in nuptial coloration, although rarely they were tolerated. Juvenile pupfish often were tolerated within the territories.

AGGREGATING BEHAVIOR

Normal schooling behavior was never observed in the inadequate space of the aquaria. However, when the pupfish were first brought in from the field and placed in an aquarium they formed schools. The fish moved slowly over the bottom in troop-like columns, often near the wall of the aquarium. After the fish had acquainted themselves with the new surroundings this behavior disappeared.

Pupfish in shore pools and springs regularly move in schools and forage in groups. The schools are spread out in the horizontal plane, but not in the vertical; according to Keenleyside (1955) this is typical for fish schools. Females and juveniles school throughout the year, and the males school with them when not holding territories. During the breeding season males not infrequently are seen in the rear parts

of otherwise all female schools. Both sexes school together during the winter. However, during the coldest weather the fish sometimes spread out to such an extent that schools are barely recognizable as such.

Pupfish of different sizes usually do not school together. They segregate into groups in which the individuals are about equal in length. Observations of schools of mixed size groups revealed that sorting results from differences in swimming speed. The larger fish swim proportionately faster, and thus heterogeneous schools quickly fractionate because the smaller fish fall behind. Also, the smaller fish stay in shallower water, almost in proportion to their sizes.

Schooling plays a greater role in the social behavior of juvenile pupfish than it does in that of adult females. The females move about in smaller numbers and also separate from the school more readily. Juvenile pupfish have been observed in schools which were estimated to number upwards of 10,000 individuals. The cohesion of even small schools of juveniles can be appreciated from the behavior portrayed in Figure 3.

A remarkably different type of schooling behavior once was observed in a mixed school of about 300 female and juvenile pupfish. The school, traveling in a tight column close to the bottom, moved into a small channel (1 m wide and 5 cm deep) which connected two

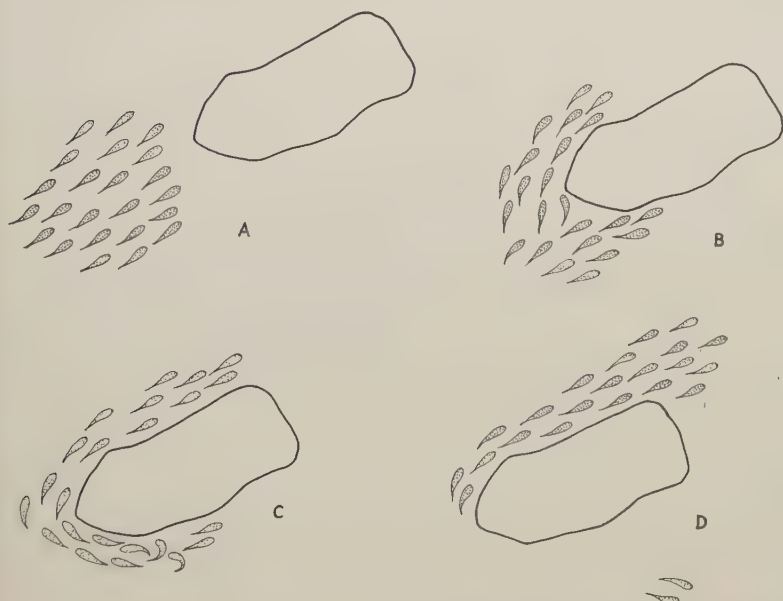


Fig. 3.—A school of juvenile pupfish in shallow water (about 2 cm deep) approach (A), and pass (B to D), a tiny island (about 10 cm long). The attraction the school holds for the individual is seen best in Panel C.

shore pools. A slight current was perceptible, but the water temperature was the same as that of each of the contiguous pools. Once in the channel the fish began to circle and formed a revolving disc-shaped school. They were uncommonly close to one another, often touching. Many different species of marine fishes which regularly school form similar compact whirling masses of fish when attacked by predators. Now and then the milling pupfish darted aside almost as one. This sudden darting, together with milling, was strikingly like the fright behavior of shoaling oceanic fishes. On the other hand the entire school of pupfish sometimes stopped suddenly and settled onto the bottom. Individuals nestled into the algal mat and lay almost motionless. They did not, however, burrow out of sight as pupfish sometimes do when escaping a net, but remained on top of the mat. Shortly thereafter they would jointly resume milling. This behavior, for which no explanation is forthcoming, lasted almost two hours.

While milling the pupfish showed marked avoidance of a shadowed area. A small pier cast a straight edged shadow which fell near the fish. If the school came up against the shadow, the near side formed a straight line along the shadow so that the fish remained in the sun-lit water. Breder and Rasquin (1950) concluded from their experiments that *Cyprinodon baconi* is, "practically light indifferent." It is not likely that two such closely related species would have such different responses to contrasting light intensities. Doubtless the environment and the emotional state of the fish can alter such responses. Breder (1959) has noted that young *Mugil trichodon* (Poey) are clearly wary of shadows in nature, but are photo-negative in the experimental choice box.

DISCUSSION

Many differences in behavior between pupfish in their natural habitat and those in aquaria could be pointed out. The obvious differences in territoriality and schooling behavior require no further comment. On the other hand, the prolonged pair bond seen between the fish in aquaria deserves further consideration. Without the benefit of field observations, one would conclude falsely that the male and female regularly form a pair which lasts for an hour or more. Further, one might think that nuzzling and meandering were important elements, not rare ones, of the reproductive behavior. Another difference is that the reaction of male and female to one another is immediate in the field. When the female is ready to spawn she seeks a fully receptive male. In the aquarium, however, the fish are suddenly together and then must become properly motivated. Thus the resident female at first attacks the introduced male. In other words, the spawning threshold is too high at first (or the fighting threshold is too low) and must be lowered before reproductive behavior can occur.

The female pupfish probably recognizes the male from his shape and color. In the shore pools females usually initiate the spawning at

the approach of a male. The ability of a female to discern, and respond to, a motionless male in a beaker of water also speaks for this argument. Nonetheless, movement by the male is doubtless also of importance.

The means by which a male pupfish recognizes a female are less clear. Breeding males attack other males, but not females, even though the female is not ready to spawn, but is only passing through his territory. Also, males do not usually attack juveniles. On the other hand, males in aquaria containing only other males occasionally spawn against their fellows. The male treated as a female is smaller, passive, and pale in color from being harassed. In the prolonged absence of a female the spawning threshold should be low. Consequently, otherwise inadequate stimuli could release this behavior. Koster (1948) observed in a free living toothcarp, *Plancterus kansae* (Garman), one male attempting to spawn against another male which was non-moving, though fully colored.

The brilliant nuptial dress of the patrolling male pupfish renders him conspicuous. And the coloration and behavior go hand in hand. As the male swims forward the movements of the orange caudal fin contrast sharply with the blue body. When the male stops, the orange pectoral fins are thrown forward and begin beating alternately. Thus the run-stop nature of patrolling shifts the flicker of orange back and forth between the pectoral and caudal fins. This type of display attracts the eye of the observer, and presumably also that of the female pupfish.

The black eyes of the male in breeding colors may be important clues in the orientation of the fighting behavior. Male pupfish start their fights facing one another, move into the eye to eye position, and then stand parallel, invariably head to tail. That they never stand parallel and head to head speaks strongly for the necessity of some structure which carries the information about the front and back ends of the opponent. Just moving ahead is not enough; one or the other male often starts circling at this time so that the other must continually orient itself to its opponent. The parallel and head to tail position can be observed in the fights of several other kinds of fishes. But many species go from the facing stance to a parallel position which is sometimes head to tail and othertimes head to head. This can be seen especially well in the common aquarium cyprinid *Brachydanio rerio* (Hamilton). The behavior of a reasonably close relative of the desert pupfish, *Fundulus notatus* (Rafinesque), however, suggests that the eye is not necessarily important in orienting rival males to one another. As described by Carranza and Winn (1954), *F. notatus* males orient head to tail even though the eye is obscured by a black horizontal line passing through it.

The color of the caudal fin also might play an important role in the fight between two male pupfish. Once they are head to tail they begin tail-beating and each sees only the orange caudal fin of the

opponent. The size and color of the tail could augment the effect of the tail-beats in intimidating the rival male.

The color pattern and behavior of the desert pupfish, *Cyprinodon macularius*, appear to be among the simplest kinds known within the toothcarps. As can be seen in any good aquarium book, male toothcarps can be arranged in a series according to the increasing ornamentation of the caudal fin and the borders especially of the median fins. One can proceed from the almost uniformly orange caudal fin found in the desert pupfish to the beautifully adorned species of *Aphyosemion*. In the closely related species, *Cyprinodon variegatus*, the caudal fin is orange, but is also bordered with black (Raney *et al.*, 1953). On the other hand, the color pattern of *Cyprinodon nevadensis* Eigenmann and Eigenmann, once considered conspecific with *macularius*, is of an even simpler type: the caudal fin is the same dark blue as the body (Miller, 1943). It would be of interest to know which selective pressures were more effective in producing these elaborate structures — intimidation of rival males, or selection by the females. The complexity of the body markings also proceeds well beyond the simple blue of the desert pupfish.

An overwhelming number of male toothcarps have brightly colored pectoral fins when reproductively motivated. It is extremely unusual for the pectoral fins of free-swimming fishes to be conspicuously colored. In most fishes, excluding the bottom living forms, the pectoral fins are hyaline. These fins are normally in constant motion to counteract the opercular jets. Moreover, they are frequently the fins most used in the normal activities of fishes. The bright markings are commonly carried on the median fins which are used less often in moving about. *Anabas testudineus* (Bloch), a labyrinth fish, and pomacentrid fishes of the genus *Amphiprion* constitute rare instances of fishes with colorful pectoral fins outside the Cyprinodontidae. Judging from its widespread occurrence, the flickering of conspicuous pectoral fins is a long established behavioral characteristic in the Cyprinodontidae.

The spawning posture of cyprinodontid fishes is a splendid preadaptation to viviparity. Rosen and Gordon (1953) have shown that the anatomy of the anal fin of the male adumbrates the evolution of the gonopodium. It is not surprising that viviparity has arisen independently within the Cyprinodontiformes at least five times, namely in the Adrianichthyidae, Anablepidae, Goodiidae, Jenynsiidae, and Poeciliidae. Many intermediate forms are known, such as *Cubanichthys*, *Horaichthys*, and *Oryzias*.

A comparison of the behavior of the desert pupfish with that of the viviparous fishes of the related family Poeciliidae will not be undertaken here. The behavior of the members of the other viviparous families is almost unknown. The reader may wish to compare the behavior of the desert pupfish with that which is known for the Poeciliidae. The article by Wickler (1957) should be useful in this respect since it treats several species of Poeciliidae.

Within the Cyprinodontidae the spawning behavior of the desert

pupfish appears to represent one of the simplest types. As with most of the toothcarps the spawning position is one in which the pair is upright, parallel, touching, S-shaped, and facing in the same direction. Unfortunately most of the information concerning the spawning behavior of cyprinodontid fishes is scattered in the literature of the aquarist, and often is in an unusable form. Nonetheless, certain types of variation are reliably evident. In some species the pair bores into the bottom (for instance, *Cynolebias*, *Pterolebias*), in others into plants (*Epiplatys*). Sometimes the spawning position includes laying over on the side, usually with the male on top (*Plancterus*, Koster, 1948). The coming together of males and females is also usually more circuitous than observed in the desert pupfish.

The complex mating ethogram of *Oryzias latipes* (Temminck and Schlegel) has been described by Ono and Uematsu (1957). Although *Oryzias* and *Cyprinodon* are not closely related, certain aspects of their behavior are remarkably similar. Ono and Uematsu have named the constituent motor patterns in *Oryzias* and listed them in their customary sequence of occurrence. The motor patterns, with their possible counterparts in the pupfish, are given in the intended sequence, but those movements peculiar to *Oryzias* are omitted: "pecking up" — nuzzling, "floating up" — sidling, "crossing" — wrapping, "copulation" — S-shaping, and "spawning" — jerking. Of the foregoing, the correspondence between "pecking up" and nuzzling seems the least certain.

The ethology of *Cyprinodon macularius* described in this article and that of *C. variegatus* as reported by Raney *et al.* (1953) appear to be essentially similar. Since these authors did not describe most of the motor patterns, little more can be said. In one respect, however, the two species doubtless differ. The males of *variegatus* make pits in their territories, most often near the territorial center. This "nest" is a roughly circular pit, 10 to 15 cm in diameter, and 2.5 to 4 cm deep. Spawning within the "nest," however, is unusual. The males of another American toothcarp, *Jordanella floridae* Goode and Bean, also make pits which are not used as incubation sites for the eggs (Peters, 1941). Males of *C. macularius* build pits only under certain conditions which have been described in the preceding. Even then the pits are appreciably smaller (about 6.5 by 2.5 cm) than those reported for *variegatus*. It might be pertinent to mention that *macularius* occurs in desert pools which seldom have a substrate suitable for pit building. Perhaps the environment has selected against this behavior in the desert pupfish.

Nipping the substrate by the female also calls for comment. This movement reveals the female pupfish definitely is ready to spawn. The motivation, therefore, is predominantly sexual. But in its form nipping clearly is eating behavior, or an only slightly modified version of it. The movement, or associated movements, differ enough from normal eating behavior to enable the male to distinguish a receptive

female within a group of foraging females. I suspect the clue lies in the way the female drops her abdomen to the bottom as she completes the nipping, as well as in the more emphatic expression of the nipping movement itself. Females usually are foraging when they encounter a male. It seems that the principle foraging movement has been slightly exaggerated and stereotyped to signal readiness to spawn.

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Eighteen New Species in the Genus *Calicurgus* Lepeletier (Hymenoptera: Psammocharidae) from Mexico, Central and South America with a Key to All the Species and Photomicrographs of the Male Genitalia and Subgenital Plates

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ABSTRACT: Eight new species are described from Mexico and Central America. The status of *Calicurgus hyalinatus* Fabricius is discussed. Nine new species are described from South America. Keys for all the known species for both sexes are given; a separate key is provided for each region. Photomicrographs of the genitalia and subgenital plates for the males of the new species and for three species previously described. A total of twelve species are treated for Mexico and Central America and twenty-three species from South America.

The genus *Calicurgus* is represented throughout most of world, but apparently the species are more numerous in the Neotropics. The species especially as represented by the genitalia and subgenital plate are a homogeneous group without too much variation in the structure. The keys are made up in two groups, one for Mexico and Central America and the Caribbean region and the other for South America. Key construction is simplified and they are easier to use when they are separate for each region. Dr. Henry K. Townes recently made a trip to the British Museum to study the type of Ichneumonidae and while there checked Cameron's types in the Cryptocheilinae. He found that *Salix teapensis* should be referred to the genus *Calicurgus* (private communication to the writer). The designations for places of deposit of the type specimens are listed below.¹

The Genus *Calicurgus* Lepeletier

This genus, one of the subfamily Cryptocheilinae, is diagnosed by the presence of straight sides of the basal abdominal segment and, in the female, teeth and spines on the outside of posterior tibiae. It is separated from the other genera by the following characters: (1) the front of the pronotum is perpendicular to the dorsal surface; (2) the anterior tibia in the female has a very noticeable spine on the dorsal apex (not so noticeable in the male); (3) the male has a

¹ Location of types: USNM = U.S. National Museum; MCZ = Museum of Comparative Zoology, Harvard University; MSU = Michigan State University, East Lansing, Michigan; RRD = R. R. Dreisbach, Midland, Michigan; Cal. Acad. = California Academy of Science, Golden Gate Park, San Francisco; Kan. = Entomology Museum, University of Kansas, Lawrence; Cal. = State Dept. of Agriculture, Sacramento 14, California.

characteristic genitalia and subgenital plate in that the volsellae have a double pair of basal hooklets on the inside edge near the base; (4) in both sexes the eyes converge strongly above; (5) the basal and transverse veins in the fore wings are either interstitial or only slightly disjointed; and (6) the subdiscoidal vein in rear wings is either interstitial with cubital vein or slightly basad of it (generally from one to two times the thickness of a vein).

In the descriptions, number in parenthesis after the lower or upper interocular distance is the comparative length on the same scale as the ratio of the lengths of the first antennal joints. This is measured by a scale in the eyepiece of the microscope and the scale is 100 divisions = 1.325 mm.

Mexican, Central American and Caribbean Species

***Calicurgus flavidus* n. sp.**

Holotype female.—Body completely black, except apical half of mandibles are reddish; legs beyond tibiae are brownish; sides of face to base of antennae with beautiful yellowish pubescence; sides of pronotum and across the posterior border with similar pubescence but not quite so yellow; the ventral surface of fore coxae, and the outer posterior corners of propodeum with a narrow band across the extreme apex the same color as face; the rest of thorax and legs with pubescence silvery; clypeus with a broad ($0.3 \times$ length of clypeus) shiny, hairless apical edge, which does not quite reach the sides; the apex of this apical edge with a very narrow smooth apical margin, the surface back of margin like rest of clypeus, opaque, hairy and with coarse punctures; this punctured edge of front margin about $0.45 \times$ width of clypeus; clypeus $2.3 \times$ broad as long; eyes strongly converging above, the lower interocular distance (95) $1.45 \times$ that of upper (65); interocular distance at middle, $0.52 \times$ the transfacial; head $1.25 \times$ as broad as long; lateral ocelli slightly closer to eyes than to each other (ratio 12:15); ratio of length of first 4 antennal joints is 35:8:70:60; front mat punctures almost touching, those on mesonotum slightly farther apart, surface opaque; pronotum transverse behind; propodeum short in a smooth curve from base to apex, no dorsal hair, except at lower outside corners; wings strongly banded over basal veins and a broader band over cubital cells, covering the marginal, second and third cubital cells and extending to rear edge of wing but hardly noticeable behind discoidal cell; the first band about as wide as third cubital cell, starting at base of basal vein and at subcostal vein; second and third cubital cells of equal length on marginal vein but third the longest below; the second recurrent vein strongly bent outward in the middle; the basal vein in fore wing basad of the transverse by a little more than $0.4 \times$ the length of latter; the pulvillus of claws large, subparallel-sided to about middle and the apical half triangular with a broad apex; apical half of pulvillus black; the apical black-shining edge of clypeus has four rather strong

lengthwise wrinkles; length head and thorax 4.0 mm, abdomen 2.7 mm, fore wing 8.7 mm, rear wing 7.1 mm.

Type locality.—Cuernavaca, Morelia, Mexico, June, 1945, N. L. H. Kraus (USNM).

Paratypes.—One, 4 miles E. of Cuernavaca, Morelos, Mexico, 6000', June 20, 1959 (RRD); another, same data but date, June 25, 1959 (Evans).

***Calicurgus niger* n. sp.**

Holotype female.—Completely black, except a tinge of dark red on apical half of mandibles; only thin fine pubescence on body, no shiny pubescence spots; clypeus like that of *C. flavidus* but front edge not as wide nor as smooth, and with a few more not so coarse wrinkles, clypeus $1.3 \times$ as broad as long; eyes strongly convergent above, lower interocular distance (80) is $1.33 \times$ the upper (60); head slightly broader than long; middle interocular distance $0.57 \times$ the transfacial distance; ratio of length of the first 4 antennal joints is 35:15:60:55; lateral ocelli as far from eyes as from each other, front and mesonotum like *flavidus* but more shining; wings banded like *flavidus* but the bands not as dark and the one over the basal veins narrower; cubital cells like *flavidus*; the basal and transverse veins in fore wings are interstitial; antennae much more slender than that of *flavidus*; pulvillus of claws the same shape as *flavidus*, but apical half white; length of head and thorax 3.3 mm, abdomen 3.0 mm, fore wing 6.0 mm, rear wing 4.3 mm.

Type Locality.—S. Andres Tuxtla, Vera Cruz, Mexico, October 25, 1957, R. and K. Dreisbach (USNM).

***Calicurgus cruralis* n. sp.**

Holotype female.—Ground color of body black, but with a deep reddish cast to the thorax, basal two abdominal segments and the posterior edge of third segment; the clypeus and mandibles a little brighter reddish; all the legs including coxae, trochanters, and apical tarsal joints a light to dark reddish; antennae wholly yellowish; a broad shining apical rim of clypeus, a narrow smooth edge and the rest of hairless rim with coarse lengthwise wrinkles, clypeus almost $3.0 \times$ as broad as long, the hairless rim less than $0.3 \times$ length in middle and becoming obsolete at sides; a number of long hairs extend from center of clypeus beyond the hairless rim; clypeus, face and lower front silvery sericeous; the whole thorax and abdomen with a thin fine silvery pubescence, which in places appears more as a bloom than a pubescence; head $1.2 \times$ as broad as long; the middle interocular distance $0.56 \times$ the transfacial the upper interocular distance (60) is $0.6 \times$ the lower; ratio of length of first 4 antennal joints is 35:15:65:55; lateral ocelli as far from eyes as from each other; wings hyaline, veins yellow, a dim cloud over basal veins (from subcostal vein backward, which fades out before reaching the hind margin of wing) and over cubital cells; the subapical cloud covers the marginal, second and third cubital cells and about one half of the

discoidal cell back of them; these clouds are very faint; basal and transverse veins in fore wings interstitial and the subdiscoidal vein in rear wing basad of cubitus by about $2.0 \times$ the thickness of vein; a few long hairs on sternum of abdomen from about fourth sternite with an increase of long light hairs on last segment; length of head and thorax 4.0 mm, abdomen 3.3 mm, fore wing 7.2 mm, rear wing 5.3 mm.

Type Locality.—Balboa, Canal Zone, Panama, May 13, 1914, T. Hallinan (MCZ).

***Calicurgus argutus* n. sp.**

Holotype female.—Whole body black, with the legs having a slight brown color; face, clypeus, spots on sides of thorax, base of propodeum and lower sides of propodeum with a slight silvery pubescence; apical half of mandibles reddish; a broad hair-less apical rim on clypeus is $0.4 \times$ the length of clypeus in the middle and narrows toward the side, disappearing at outer 0.2 of clypeus; clypeus $2.4 \times$ as broad as wide; upper interocular distance $0.7 \times$ the lower; middle interocular distance $0.6 \times$ the transfacial; ratio of lengths of the first 4 antennal joints is 25:15:55:45; lateral ocelli slightly closer to eyes than to each other; wings hyaline except for the two clouds, apex of wing clear; cloud over basal veins small and faint, beginning behind the junction of cubital and basal vein and widening in the second discoidal cell; the cloud over the cells is much darker and larger, and covers the marginal, second, and third cubital and most of third discoidal cell; basal vein in fore wing is basad of transverse vein by about the thickness of a vein; the subdiscoidal vein in rear wings is basad of cubitus by about $2.0 \times$ the thickness of the vein; length of head and thorax 3.3 mm, abdomen 2.6 mm, fore wing 5.3 mm, rear wing 3.9 mm.

Type Locality.—Acayucan, Vera Cruz, Mexico, Oct. 23, 1957, R. and K. Dreisbach (USNM).

Paratype.—Guadalajara, Mexico, July 12, 1959, 5000', H. E. Evans (Evans).

***Calicurgus major* n. sp.**

Holotype female.—Completely black except for some reddish color on middle of mandibles, and the reddish colored spines on all the tarsal joints; strongly silvery sericeous on clypeus and face, but not on front or vertex; strongly sericeous on under side of thorax and on ventral surface of coxae; sides of thorax, and across the basal and apical surface of propodeum are strongly sericeous; the surface across middle of propodeum lacks this pubescence; the dorsal surface of propodeum, and the subcostal cell and stigma has a dull greenish color; the apical third of clypeus hairless, deep black and shining, with about 5 very large shallow pits or punctures; the hairless apical margin narrows toward the sides and becomes obsolete before reaching sides; clypeus $2.6 \times$ as wide as long; head $1.25 \times$ as broad as long; middle interocular distance $0.56 \times$ as long as transfacial; lower

interocular distance (140) $2.0 \times$ the upper (70), thus the eyes very strongly converging above; ratio of length of first 4 antennal joints is 55:20:120:100, thus third antennal joint is $1.4 \times$ as long as upper interocular distance; lateral ocelli slightly farther from each other than from the eyes (17:13); wings bifasciate with dark color; the basal band starting at subcostal vein, narrow there and expanding to greatest width at the submedian vein where it is as wide as second and third cubital cells and irregular on both edges; the band over cells covers marginal, second and third cubital and most of apical half of third discoidal cells; second recurrent vein bowed outward in the middle; tip of wing beyond cells snow-white; the wing hyaline except for the bands and apical spot; pronotum transverse on posterior edge; slight silvery pubescent spots on sides of second, third and fourth tergites; the abdomen with a slight greenish tint; posterior tibiae with 10 teeth on basal 0.75, concave on front, located on center of dorsal surface at a slight angle and with a spine behind them; another row of spines occur close to them on inner side and a row of smaller reddish spines on the outside but not so close to teeth; length of head and thorax 6.6 mm, abdomen 5.6 mm, length fore wing 11.6 mm, rear wing 8.6 mm.

Type Locality.—Mexico, Vera Cruz, Vulcan, San Martin, SE. slope 4000', July 22, 1959, at light, B. T. B. Valentine (USNM).

***Calicurgus pruinus* n. sp.**

Holotype female.—Black; apex of mandibles reddish and apex of fore tibiae and the apices of fore tarsal joints yellowish; all tarsal joints with yellowish pubescence and reddish spines; clypeus and face strongly silvery pubescent, the front with pubescence not nearly so dense; posterior orbits and sides of thorax and propodeum (except central part) are silvery pubescent; abdomen pruinose; lower side of pronotum and just below the shoulders possess two spots of pubescence (in certain light) which have a yellowish tint; apical edge of clypeus bare and with about 10 rather broad smooth longitudinal ridges; clypeus $3.0 \times$ as wide as long; lower interocular distance (90) $1.8 \times$ the upper (50); middle interocular distance $0.58 \times$ the transfacial; head $1.2 \times$ as broad as long; lateral ocelli as far from eyes as from each other; ratio of length of first four antennal joints is 40:15:70:60; pronotum transverse behind (very slightly concave); propodeum very short in a steep curve; wings bifasciate, with two dark prominent bands; the basal band, irregular on front and rear, starts just basad of basal vein and is about $0.67 \times$ as wide as the length of the second and third cubital cells on the marginal vein; the second band covers the marginal and extends to rear of wing about width of the marginal cell; the rest of wing slightly yellowish with a snow-white tip just beyond third cubital cell; quite a few long light hairs are present on the last abdominal segment, a few on the rest of the ventral segments; length of head and thorax 3.6 mm, abdomen 3.3 mm, length of fore wing 6.9 mm, rear wing 5.0 mm.

Type Locality.—Acayucan, Vera Cruz, Mexico, Oct. 23, 1957, R. R. and K. N. Dreisbach (USNM).

Paratype females: Three, same data as holotype (R.R.D.); One, Yucatan, G. F. Gaumer (Kan.).

***Calicurgus albosignus* n. sp.**

Fig. 1

Holotype male.—Mostly black with the exceptions as noted below; clypeus, mandibles (except light reddish apex), mouth parts, apical 0.75 of ventral surface of fore coxae, posterior edge of pronotum, the lower front corners of pronotum, last tergite, all tibial spurs, and a ring around base of posterior tibiae, white; all femora (except extreme base of fore pair), first 2 pair tibiae (second pair slightly dark), and under side of antennae, rufous; fore tibiae blackish on last 3 joints and all of the last 2 pair black, as well as the last pair of tibiae (except basal ring); face and clypeus slightly silvery sericeous, little pubescence or hair elsewhere on body; head $1.3 \times$ as broad as long; upper and lower interocular distance equal (48); the interocular distance in middle of front greater (55); wings hyaline, no trace of a cloud; basal and transverse vein in fore wings almost interstitial, first recurrent meets second cubital cell at center, the second meets third cubital cell beyond middle; subgenital plate of the usual rectangular shape but genitalia is much different; parameres not scalloped and with a concavity outside but straight sided with a row of thick hairs on inside apical half; volsellae short, with a broad blunt apex and no sharp tooth on inside near middle; length head and thorax 3.0 mm, abdomen 2.6 mm, fore wing 4.3 mm, rear wing 3.3 mm; genitalia 0.66 mm, width 0.53 mm, length subgenital plate 0.78 mm (including stem), width 0.26 mm.

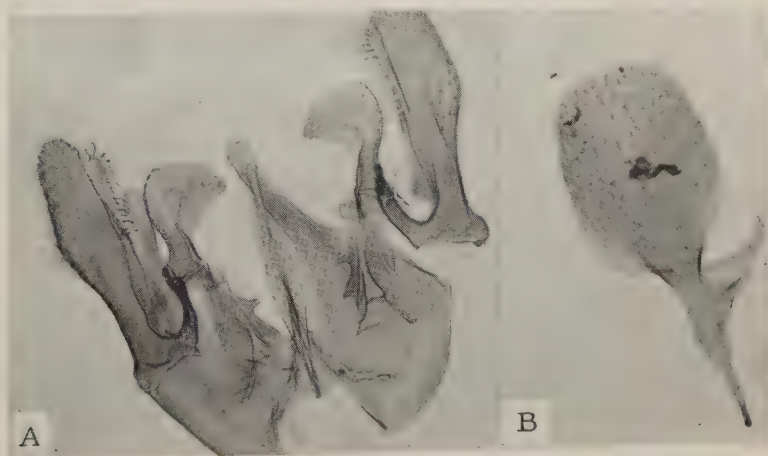


Fig. 1.—*Calicurgus albosignus*, n. sp. A. Genitalia ($\times 80$).
B. Subgenital plate ($\times 60$).

Type Locality.—Summit, Panama Canal Zone, October, 1946, N. L. H. Kraus (USNM).

Calicurgus aberrans n. sp.

Holotype male.—Body black except as noted; apex of mandibles reddish; a spot on ventral apex of fore tibiae, last tergite and tibial spurs white; apex of fore femora in front rufous; fore tibiae yellowish underneath, black above; first 3 joints of fore tarsi slightly yellowish, the last 2 pair tarsi slightly brownish; antennae wholly black; face and clypeus silvery pubescent and some silvery pubescence on mesopleura; clypeus with a narrow hairless rim and truncate across apex; clypeus a little more than $2.0 \times$ as broad as long; head as broad as long; middle interocular distance $0.61 \times$ the transfacial distance; the lower interocular distance (65) slightly greater than the upper; lateral ocelli about as far from eyes as from each other; a weak narrow infuscation over basal and transverse veins in fore wing, very short; a strong band over marginal, second and third cubital and apical third of third discoidal cells; rest of wing hyaline with the apex beyond cells hyaline but not snow-white; first and second recurrent veins meeting second and third cubital cells, respectively, beyond middle and at middle; subgenital plate differs from those of other species in genus, in being broader at apex than base; genitalia also much different; the parameres have a broad flange outside at base; volsellae end in a plate (not in a point as other species) with long hairs, and no spine on their inside near middle; the basal booklets at base of volsellae are very small, almost obsolete; the parapenial lobes are expanded at apex.

Type Locality.—San Cristobal, Casas, Chiapas, Mexico, April 30, 1959, 7500', H. E. Evans (USNM).

Paratype Males.—Three, same date as type (H. E. Evans); One, Rosario, San Juancito Mts, Honduras, 4800-5150', July 29, 1930, Hond. Exp. (ANSP); One, 4 miles E. Cuernavaca, Morelos, Mexico, June 7, 1959, 7500', (H.E.E.),

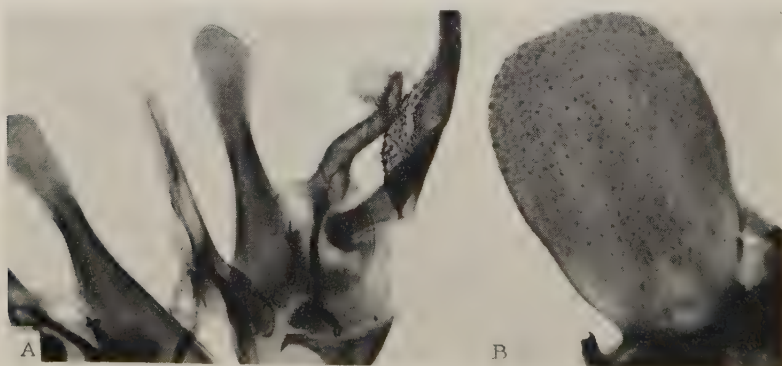


Fig. 2.—*Calicurgus aberrans*, n. sp. A. Genitalia ($\times 58$).
B. Subgenital plate ($\times 58$).

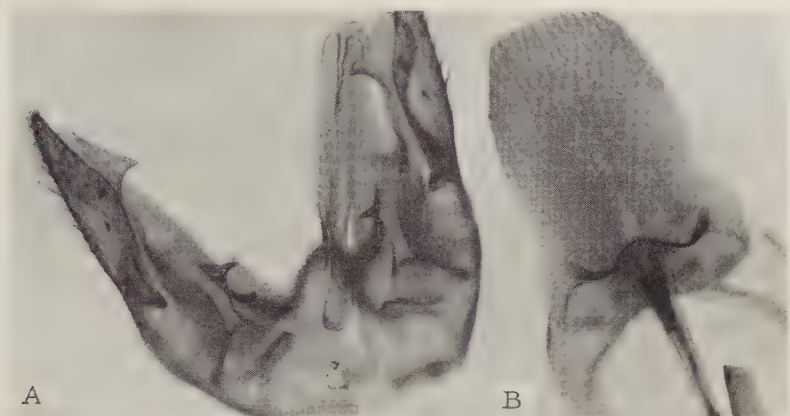


Fig. 3.—*Calicurgus hyalinatus* (Fabricius). A. Genitalia ($\times 62$).
B. Subgenital plate ($\times 62$).

June 2, 1959, 6000'; H. E. Evans (R.R.D.); One, Cuernavaca, Morelos, Mexico,
June 7, 1959, 5500' (Evans); One, San Cristobal 1), Casas, Chiapas, Mexico,
April 25, 1959, 7500', H. E. Evans (Evans).

Calicurgus hyalinatus (Fabricius)

Fig. 3

Townes (1957) considered the European *Calicurgus hyalinatus* (Fabricius) as conspecific with the polytypic Nearctic species *C. alienatus* Smith. If only the external anatomy is examined there is no reason to consider them as distinct species. However, when the genitalia is examined there is a major difference between these two entities. The volsella of the Nearctic species and the three subspecies has a strong sharp tooth about the middle of the concavity on the inside edge. This tooth is sharp and strong (Fig. 4). On the other hand the Palearctic *C. hyalinatus* has not even the trace of a tooth (Fig. 3). For this reason, I consider these entities as distinct species.

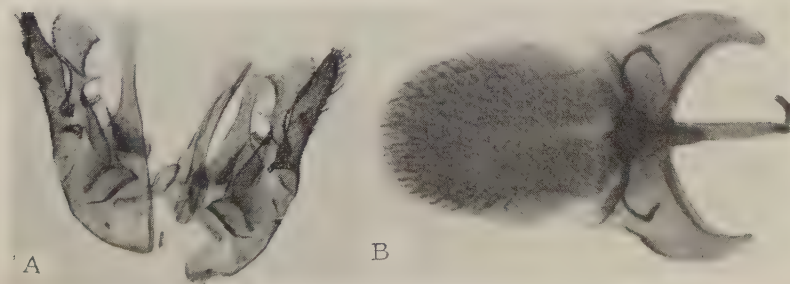


Fig. 4.—*Calicurgus alienatus alienatus* (Smith). A. Genitalia ($\times 60$). B. Subgenital plate ($\times 60$).

Key to Mexican and Central American Females

1. Abdomen entirely black 2
1. Abdomen with at least the basal two segments ferruginous 9
2. Legs completely rufous, including coxae, trochanters and tarsi (completely); fore wings with a very faint cloud over the basal veins (beginning just basad of basal vein) its length equal to length of second cubital cell on marginal vein; a similar faint cloud over all the marginal cell the second and third cubital cells and the discoidal cell just behind them; otherwise wings hyaline; basal and transverse veins in fore wings interstitial; antennae wholly yellow. Panama. *cruralis* n. sp.
2. Legs black or fore tibiae and tarsal joints very slightly brownish; at least the cloud over the cubital cells is very strong and dark; or whole wing dark 3
3. Fore wings practically wholly dark from base or close to base, an apical dark cloud and a preapical whitish band; a light streak part way across wing just back of base of stigma; rear wings fuscous.....
..... *alienatus excocetus* Townes
3. Fore wings with a cloud over basal veins and another over marginal and cubital cells or the basal cloud absent or almost so 4
4. Cloud over basal veins very faint and starts back of junction of basal and cubital veins, becoming wider as it extends backward; basal vein basad of transverse by less than the thickness of a vein; the subdiscoidal vein in rear wings basad of the cubitus by about twice the thickness of a vein; only strongly sericeous on the anterior orbits on the face (from antennae to eyes). Mexico..... *argutus* n. sp.
4. Cloud over basal veins strong and dark, the cloud extending over the junction of the basal and cubital cells to the subcostal vein; the cloud over the cubital cells stronger 5
5. The dense glistening pubescence on sides of face and across posterior edge of propodeum (especially) with light golden color; apical 0.25 of clypeus hairless, shining and with lengthwise wrinkles (about 5 large ones); apex of wings beyond cells snow white in reflected light; the basal vein basad of transverse in fore wings by width of vein, in rear wings subdiscoidal basad of cubitus by width of vein; basal cloud only as wide as length of second cubital cell on marginal vein. Mexico. *flavidus* n. sp.
5. The pubescence silvery with no trace of golden color; clypeus with or without the wrinkles 6
6. Basal cloud as broad as the combined lengths of second and third cubital veins on marginal cells, and full width straight across wing; front with a silvery pile, thorax white with silvery pile; legs densely silvery-pruinose; first transverse cubital vein slightly elbowed at base; almost 11.0 mm long. Mexico..... *teapensis* Cameron
6. Basal cloud not much broader than length of second cubital cell on marginal vein; legs not densely silvery-pruinose; front and sides of thorax not as strongly silvery as in preceding; much smaller size, less than 10.0 mm long 7
7. Rather strongly silvery, the abdomen pruinose; lower interocular distance 1.5× the upper; in reflected light wing shows up strongly dark in banded area; intermediate in size between the next 2; lateral ocelli slightly nearer each other than to the eyes; size 7.0 to 10 mm. Mexico. *pruinosis* n. sp.
7. Not silvery pubescent, (1) upper and lower interocular distance same as above and lateral ocelli *same as above*; size *smaller*, or (2) if size larger then lower interocular distance is 2.0× the lower 8

8. As in (1) above, size less than 7.0 mm; black area over cubital cells covering a greater part of wing. Mexico. *niger* n. sp.
 8. As in (2) above, size 12.2 mm. Mexico. *major* n. sp.
 9. Abdomen black apically; posterior tibiae with some infuscation at its apical one-quarter. U.S. and Mexico. *alienatus alienatus* Smith
 9. Abdomen entirely rufous; posterior tibiae entirely rufous except for a little darkening on its apical one-tenth. U.S. and Mexico.
 *alienatus rupe*x Cresson

Males

1. Femora and tibiae of middle and hind legs black 2
 1. Femora and tibiae of middle and hind legs more or less ferruginous 3
 2. Posterior margin of pronotum with a white band; wings *not* bifasciate, with a narrow dark band over basal veins and a very prominent one over marginal and second and third cubital cells; front tarsi and front of fore tibiae tan, tibial spurs and a spot on rear apex of front tibiae white; parameres with a sharp point on inside of apex and one about middle on inside; subgenital plate almost rectangular. U.S. and Mexico.
 *alienatus excoc*tus Townes
 2. Posterior margin of pronotum black; wings bifasciate, with a narrow rather faint band over basal veins and a strong one over the cubital cells; fore tarsi and *hind* part of fore tibiae tan, with fore part of front tibiae darker; parameres very blunt and broad at apex on inside and no trace of tooth on inside near middle; the 2 basal hooklets near base on inside of volsellae hardly more than indicated almost obsolete; subgenital plate wider at apex than base; spurs white. (Fig. 2.) *aberrans* n. sp.
 3. Clypeus entirely white; the fore coxae white on apical 0.75 underneath and a white spot on lower front corners of pronotum; all femora ferruginous except extreme base of first pair are fuscous; genitalia with parameres straight sided and with a row of short thick hairs on inside on apical half; apex of volsellae blunt without a tooth and no sharp tooth about middle on inside; basal hooklets on base of volsellae very small. (Fig. 1.) *albosignus* n. sp.
 3. Clypeus with some black; fore coxae without white; no white spot on lower front corners of pronotum; femora generally with more infuscation; parameres with a deep concavity on outside; volsellae with an acute tooth at apex and also one on inside near middle; the 2 pair of basal hooklets strong 4
 4. Femora, tibiae, fore and middle tarsi fulvous to light brown; the femora basally infusate; the middle and especially the hind tibiae, more or less infusate apically and basally; the extent of basal infuscation on femora varies from a narrow basal ring to more than 0.6 the length; the infuscation is usually most extensive on front femora. U.S. *alienatus borealis* Banks
 4. Colored as in *borealis* except for an average smaller extent of infuscation on femora and tibiae. (Fig. 4.)
 *alienatus alienatus* Smith and *alienatus rupe*x Cresson

The South American Species
Calicurgus ruficrus n. sp.

Fig. 5.

Holotype male.—Head, thorax and last four abdominal segments black; clypeus except central 0.25 white; a yellowish posterior border



Fig. 5.—*Calicurgus ruficrus*, n. sp. A. Genitalia ($\times 80$).
B. Subgenital plate ($\times 80$).

on pronotum; ventral surface of first abdominal segment rufous as well as all the second and third (posterior border of second and third segment and dorsal surface of first blackish); last tergite with a dorsal white spot; mouth parts yellowish; all trochanters, femora and tibiae rufous; fore coxae mostly blackish, the last 2 pair rufous; last joint of first 2 pair tarsi brownish; last pair completely brown, as well as apex of last pair tibiae; first pair spurs whitish, the last 2 pair almost pure white; upper and lower interocular distance equal (55); wings hyaline, the third intercubital vein rather suddenly bent forward thus making third cubital cell shorter on marginal vein than the second, about $0.6 \times$ as long; basal and transverse veins in fore wings slightly disjointed; thorax very finely, silvery pubescent; antennae black above, brown beneath; lateral ocelli as far from eyes as from each other; head, front, and mesonotum finely punctured; genitalia and subgenital plate similar to *C. hyalinatus alienatus*; length head and thorax 3.0 mm, abdomen 3.0 mm, fore wings 5.3 mm, rear wings 4.0 mm, length genitalia 0.53 mm, width 0.26 mm, length subgenital plate 0.33 mm, width 0.26.

Type Locality.—Nova Teutonia, Santa Catarina, Brazil, November 29, 1955, Fritz Plaumann (Townes).

Paratypes.—Fifteen from Nova Teutonia, Santa Catarina, Brazil, Fritz Plaumann, with dates as follows: one, Nov. 27, 1956 (Townes); two, Nov. 29, 1955 and two, Nov. 26, 1953 (RRD) (Townes); one, Nov. 18, 1956 and four, Dec. 25, 1953 (Townes); one, Dec. 2, 1953 (Townes); one, Jan. 6, 1957 (MCZ); one, Dec. 3, 1955 (Townes); one, Dec. 25, 1952 (Townes); one, Dec. 4, 1955 (USNM); one, Nova Teutonia, Brazil, March 24, 1951 (Cal.).

Calicurgus unifascias n. sp.

Fig. 6

Holotype male.—Head, thorax, abdomen and legs black except

as noted below; mentum, white on sides of clypeus for about 0.6 of width, lower edges of pronotum, the outer posterior dorsal corners of pronotum, the last tergite of abdomen, the ventral apical half of fore coxae, the apical edge of basal spot on outside of posterior tibiae and the basal half of mandible (apical half reddish); last 3 joints of maxillary palpi and last 2 joints of labial palpi, white; basal 2 joints of maxillary palpi and basal one of labial palpi, brown; the first 2 segments of abdomen slightly reddish on sides; abdomen flattened; antennae black on dorsal surface and on first 2 joints beneath, rest brown beneath; front and vertex of head and thorax with a dull bluish color, shining; head and mesonotum very finely punctured; face, clypeus, and lower anterior orbits finely, silvery, pubescent; thorax and abdomen also finely pubescent; wings hyaline, with a faint, narrow darkening of the basal veins, and a fairly strong cloud covering the marginal cell, most of second and third cubital cells and extending into discoidal cell slightly; third cubital cell not quite as long as the second on the marginal vein but slightly longer than second below; basal and transverse veins in fore wings interstitial as are the cubitus and subdiscoidal in rear wings; upper and lower interocular distances equal (60) lateral ocelli as far from eyes as each other; genitalia distinctive, the parameres with three scalloped cross ridges on outside, and broader than usual; the volsellae without a sharp tooth about middle on inside; subgenital plate broader than usual; length of head and thorax 3.0 mm, abdomen 2.6 mm, fore wing 6.8 mm, rear wing 5.3 mm, length genitalia 0.79 mm, width 0.66, length subgenital 0.86 mm, width 0.40 mm.

Type Locality.—Nova Teutonia, Santa Catarina, Brazil, December 8, 1953, Fritz Plaumann (Townes).

Paratypes.—One, same locality, Dec. 26, 1952 (RRD); another, same locality, December 8, 1953 (USNM); two, V. Padro Monti (R. A. Tucuman-Burruyacu), 17.1, July 11, 1946, R. Golbach (MCZ) (RRD).



Fig. 6.—*Calicurgus unifascias*, n. sp. A. Genitalia ($\times 48$).
B. Subgenital plate ($\times 48$).



Fig. 7.—*Calicurgus anomalus*, n. sp. A. Genitalia ($\times 60$).
B. Subgenital plate ($\times 60$).

***Calicurgus anomalus* n. sp.**

Fig. 7.

Holotype male.—Head black, thorax a dark brown, abdomen about same color as thorax but the sides and ventral surface of first 2 segments are yellowish; coxae, trochanters, and femora same color as thorax; outside of fore tibiae and last two pair of tibiae same color, except the last 2 pair tibiae have the dorsal base white; tarsal joints about same color, except first pair have their apex yellowish; a white stripe across posterior border of pronotum; sides of clypeus with white spots which do not quite reach base of clypeus, the color covering about 0.25 of width of clypeus; apex of fore coxae white; clypeus $2.5 \times$ as broad as long; middle interocular distance). $60 \times$ the transfacial; head $1.1 \times$ as broad as long; lower interocular distance (50) about equal to the upper; ratio of length of first 4 antennal joints is $25:12:22:22$; lateral ocelli slightly nearer the eyes than each other; a stripe of silvery pubescence on anterior orbits above the white spots on side of clypeus which extends above base of antennae; very little pubescence on rest of body; pronotum transverse behind; wings hyaline slightly brownish; transverse and basal veins in fore wings interstitial, subdiscoidal in rear wings basad of cubitus; subgenital plate broad for its length; genitalia much more hairy than that of any other species I have seen from the western hemisphere; parameres very broad and flat, with long hairs on inside and around apex; these are visible and diagnostic without dissection; volsellae with the apex heavier and longer than usual and the spine on the inside about the middle hardly more than indicated where usually it is large and sharp; length head and thorax 3.6 mm, abdomen 3.0 mm, fore wing 5.3 mm, rear wing 3.4 mm, length genitalia 0.73 mm, width 0.50 mm, length subgenital plate 0.60 mm, width 0.33 mm.

Type Locality.—Nova Teutonia, Santa Catarina, Brazil, November 2, 1955. Fritz Plaumann (Townes).

Paratypes.—One, same locality, November 19, 1955 (RRD); two, same locality, January 10, 1956 and December 15, 1953 (Townes).

***Calicurgus ornatus* n. sp.**

Holotype female.—Whole body and legs black (exceptions noted below) with the patches of silvery pubescence making a beautiful appearance; apical half of mandibles a deep red; the patch of pubescence at apex of posterior tibiae, on the inside, reddish and tarsal joints are all slightly reddish with the apex of the joints slightly more colored than the other parts; the apical tergite also reddish; face, clypeus (except apical margin), and inner orbits to just above antennae with prostrate dense silvery pubescence in reflected light; the coxae, above and below, more or less, the mesopleura, and a band across apical half of propodeum (also a slight longitudinal band on dorsum) with strong glistening pubescence on sides and as streaks on dorsal surface; the clypeus with a black shining rim 0.4 of its length in middle which narrows and almost disappears at sides; clypeus $2.3 \times$ as broad as long; head not quite $1.2 \times$ as broad as long; lower interocular distance (115) almost $2.0 \times$ the upper (60), thus the eyes strongly converging above; interocular distance at middle $0.58 \times$ the transfacial distance; ratio of length of first 4 antennal joints is 60:20:95:75; lateral ocelli as far from eyes as from each other; pronotum almost transverse on posterior border but a slight indentation in center and a faint groove longitudinally on dorsum in center; wings hyaline but with two dark bands; the first band from subcosta backward over basal veins to rear of wing about $0.6 \times$ as wide as the one over cells; the apical band covers marginal cell, the second and third cubital cells and extends through the discoidal cell; basal vein slightly basad of transverse vein in fore wings by about the thickness of the vein; second and third cubital cells of equal length on marginal vein, but the third longer on base than the second; the second recurrent vein strongly bowed outward in the middle; the subdiscoidal vein in rear wing basad of cubitus by the width of vein; a few long hairs on propodeum, on apical margins of last three sternites, and on the last 2 tergites; posterior tibiae with 10 large concave teeth on dorsal surface, with a few fine hairs, shining and with a large spine behind each one, which is about $3.0 \times$ as long as the height of apex of tooth; a row of spines on outer edge of tibia as long as the spines behind teeth; the large spine on apical dorsal tip of fore tibiae is red on basal third, the rest deep black; the apex of tibiae is reddish; length head and thorax 5.0 mm, abdomen 6.3 mm, fore wing 8.8 mm, rear wing 6.9 mm.

Type Locality.—Monson Valley, Tingo Maria, Peru, October 26, 1954, E. L. Schlinger and E. G. Ross (Cal. Acad.).

***Calicurgus anthracinus* n. sp.**

Holotype female.—A deep shining black, over the whole body including the coxae; trochanters slightly rufous especially below and on apex; all femora, tibiae and first 2 pair metatarsal joints rufous; last 4 joints of the first 2 pair legs and all the joints of last pair a reddish black; mouth parts, the fore coxae, and the apex of abdomen with considerable long hairs; a few long hairs on the posterior edges of all abdominal ventral segments; apical margin of clypeus hairless, shining and with a few longitudinal coarse wrinkles, for about 0.3 of length in center; the hairless rim becoming shorter at the sides; clypeus $2.5 \times$ as broad as long; head $1.1 \times$ as broad as long; middle interocular distance $0.66 \times$ the transfacial; lower interocular distance $1.33 \times$ the upper (90); lateral ocelli not quite $2.0 \times$ as far from eyes as each other; ratio of lengths of first 4 joints of antennae is 40:15:100:80; antennae entirely black; pronotum transverse behind; fore wings deep black with a brilliant violaceous reflection; rear wings deep brown without so much reflection; in fore wings basal vein basad of transverse vein by about $0.5 \times$ length of the latter; in rear wings the subdiscoidal vein is very slightly basad of cubitus; in fore wing third cubital cell is longer than second, the latter rectangular and longer than broad (55:80); the second recurrent vein strongly bent outward (angled) in the middle; length head and thorax 5.6 mm, abdomen 5.9 mm, fore wing 9.6 mm, rear wing 6.9 mm.

Type Locality.—Argentina, B. Aires City, March, 1950, M. A. Fritz (USNM).

***Calicurgus semirufus* n. sp.**

Holotype female.—Head, thorax and last three abdominal segments black, the head and thorax dull, the last three abdominal segments shining with a bluish tint; the thorax also has a dull bluish luster in certain light; the first 2 abdominal segments rufous both above and below, except the extreme base of the first one is black; the first 2 segments are also shining; coxae black with bluish luster, the trochanters blackish with the tips rufous; all femora, tibiae and all tarsi (except last joint) same rufous color as base of abdomen; the apical 0.4 of clypeus with very large coarse punctures except the very narrow apical rim; clypeus $2.4 \times$ as broad as long; head $1.1 \times$ as broad as long; middle interocular distance $0.50 \times$ the transfacial; lower interocular distance $1.3 \times$ the upper (95); lateral ocelli slightly farther from eyes than from each other; ratio of length of first 4 antennal joints is 40:15:75:70; pronotum transverse behind, dorsal part very short; propodeum very short in a smooth steep curve, the dorsal part about $0.5 \times$ the posterior slope; fore wings very deep brown, rear wings brown but lighter; basal vein basad of transverse by less than width of vein, the subdiscoidal vein in rear wings basad of cubitus by the width of vein; second cubital cell almost square longer than wide by ratio of 10:9; third cubital cell almost $2.0 \times$ as

long as second; second recurrent vein in fore wings bent outward in a smooth curve; length of head and thorax 5.0 mm, abdomen 4.0 mm, fore wing 8.2 mm, rear wing 7.0 mm.

Type Locality.—Concepcion, Chile, 1904, P. Herbst (MCZ).

Paratype.—Chile, Varos (RRD); another, Angol, Chile, Dec. 22, 1956, Shoz (MSU).

***Calicurgus chilensis* n. sp.**

Fig. 8.

Holotype male.—Completely dull black, except for two white bands across the front of clypeus, just back of the narrow black hairless rim, which do not quite touch in middle; clypeus $2.0 \times$ as broad as wide; the white stripe covers about 0.25 of length of clypeus; the clypeus has a comparative width of 85, but the front quarter is suddenly narrowed at the posterior edge of the white band so that the part covered by the white band is only $0.7 \times$ as wide as the part between the eyes; the whole head densely covered with long black hair; the first antennal joint below and the upper side of all the coxae covered with some long hair; the pronotum and propodeum with shorter hair; face and clypeus with silvery pubescence; wings blackish; basal vein in fore wings basad of the transverse by the thickness of a vein, and in rear wings the subdiscoidal and cubital veins are interstitial; second cubital cell rectangular only slightly longer than broad, shorter than the third; third intercubital suddenly slightly bent inward at apex marking the length of third cubital cell on marginal vein only about 0.5 that on cubital vein; interocular distance in the middle $0.63 \times$ the transfacial; lower interocular distance (85) slightly greater than the upper (80); head $1.2 \times$ as broad as long, lateral ocelli $1.2 \times$ as far from each other as from the eyes; head and thorax length 4.6 mm, abdomen 5.0 mm, length fore wings 7.2 mm, rear

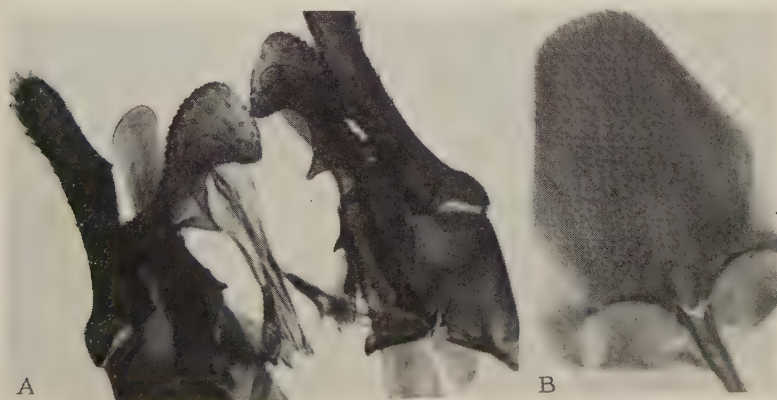


Fig. 8.—*Calicurgus chilensis*, n. sp. A. Genitalia ($\times 48$).
B. Subgenital plate ($\times 48$).

wings 6.0 mm, length genitalia 1.0 mm, width 0.66 mm, length subgenital plate 0.93 mm, width 0.46 mm.

Type Locality.—Angol, Chile, November 16, 1933 (MCZ).

***Calicurgus fuscus* n. sp.**

Holotype female.—Body black, the thorax with a bluish tint or reflection especially on the front slope of pronotum and the sides of propodeum; the middle of mandibles reddish and a slight reddish tint on the fore part of clypeus; the posterior border of tergites 1-5, as well as posterior edge of the side pieces and a lengthwise streak on side of first tergite, rufous; the visible part of last tergite rufous; all coxae, trochanters (except yellowish apex), fore femora (except knees), about basal third of mid-femora and base of posterior femora black; all of rest of legs reddish; antennae yellowish brown; clypeus, face, fore coxae in front, mesopleura, sides of pronotum and most of propodeum (in certain light) finely densely silvery serviceous; the dorsal surface of pronotum only slightly silvery, and the vertical slope in front, hairless and shining; clypeus concave in front in middle, a rather broad, smooth, hairless semi-opaque apical margin back of which is an opaque rougher hairless shining surface which makes up one half the length of clypeus; just at base of this shining apical surface is a row of long thin hairs (about 20) which extend forward beyond the margin; clypeus $2.5 \times$ as broad as long and does not quite reach the eyes; head $1.15 \times$ as broad as long; middle interocular distance $0.6 \times$ the transfacial; lower interocular distance $2.0 \times$ the upper (60) thus the eyes strongly converging above; ratio of lengths of first 4 antennal joints is 50:15:90:70; lateral ocelli slightly farther from each other than from the eyes (15:13); dorsal surface of pronotum very short, posterior border transverse; very short dorsal surface on propodeum, slope steep, no upright hairs on surface; wings hyaline with a brown tinge; basal vein basad of transverse vein in

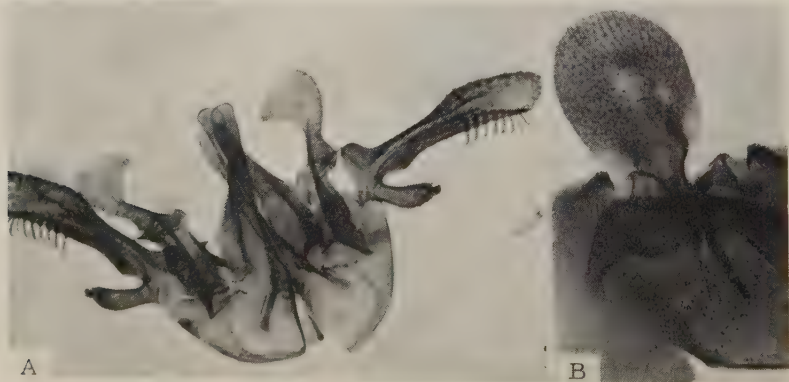


Fig. 9.—*Calicurgus modestus* (Smith). A. Genitalia ($\times 48$).
B. Subgenital plate ($\times 48$).



Fig. 10.—*Calicurgus rufigaster* Banks. A. Subgenital plate ($\times 50$).
B. Genitalia ($\times 50$).

fore wing by the width of a vein in rear wing subdiscoidal vein is basad of cubitus by about $2.0 \times$ the thickness of a vein; first intercubital vein is straight and slopes very strongly toward apex of wing, the recurrent veins meet their respective cubital cells at the apical and basal thirds respectively; nine very strong, concave, hairless teeth on middle of dorsal surface of posterior tibiae (on basal 0.6) behind the teeth is a strong sharp spine, $3-4 \times$ the length of teeth; a row of smaller spines on outer edge and a row of still smaller spines on inner edge; length head and thorax 4.6 mm, abdomen 3.5 mm, length fore wing 8.8 mm, rear wing 6.6 mm.

Type Locality.—Petropolis Rio, Brazil, March, 1938, Yellow Fever Service, MES Brazil, R. C. Shannon (USNM).

Calicurgus braziliensis n. sp.

Holotype female.—Antennae, thorax, and head black except mouth parts are brown and the apical three quarters of the mandibles are reddish; abdomen black except basal two and one-half tergites are rufous on dorsum and sides, the first 2 ventrite mostly black, the third rufous; the last pair femora rufous, the first 2 pair slightly so at apex; all the tibiae rufous beneath, the first 2 pair black above, the last pair rufous on basal half above; tarsi blackish; a few long hairs on clypeus, under head, on ventral surface of abdomen and on last tergite; clypeus short, truncate in front, with a slightly turned up rim in front, almost $3.0 \times$ as broad as long; middle interocular distance $0.60 \times$ as long as the transfacial; head as long as broad; lower interocular distance (100) a little more than $1.2 \times$ the upper (65); lateral ocelli about as far from eyes as each other; ratio of length of first 4 joints of antennae is 35:15:60:45; pronotum with the dorsal surface a flat rectangle the posterior edge transverse; fore wing with section basad of basal veins and the apex beyond cells hyaline the space be-

tween dark brown, the rear edge of the fore wing is brown to base; rear wings with apical half darker than the hyaline basal half; dorsal surface of posterior tarsi with fairly large transverse plates (concave on front) as teeth on about basal 0.7, each tooth with a spine just behind it; length head and thorax 4.0 mm, abdomen 3.6 mm, fore wing 6.5 mm, rear wing 5.5 mm.

Type Locality.—Nova Teutonia, Brazil, April 23, 1951, Fritz Plaumann (Cal.).

Key to South American Species

Females

1. Abdomen with 2 basal segments rufous; wings black, or hyaline at base and apex with space between basal veins and apex of third cubital cell darker 2
1. Abdomen wholly rufous or only the basal segment dark, or at least with 1 segment dark besides the basal 3
2. Wings black; legs completely reddish yellow beyond the trochanters; first 2 abdominal segments completely rufous. Chile. *semirufus* n. sp.
2. Wings hyaline before basal veins and beyond cubital cells, the space in between a dark brown; the first 2 segment of abdomen mostly black beneath. Brazil. *braziliensis* n. sp.
3. Abdomen wholly rufous, or only basal segment dark 4
3. Abdomen with at least 1 segment black besides the basal 6
4. Legs including coxae rufous. Paraguay. *fratellus* Holmberg
4. Coxae and trochanters black or all the legs black 5
5. Coxae and trochanters black, rest of legs rufous; wings banded. Colombia. *rufigaster* Banks
5. Legs wholly black; basal abdominal segment partly black; wings nearly evenly dark. Ecuador. *loranthe* Banks
6. Abdomen yellowish on first and second segments; venter partly pale 7
6. Abdomen black on all segments 9
7. Pronotum yellowish on hind border 8
7. Pronotum not yellowish behind; legs black, except hind femora and tibiae are rufous. Argentina, Brazil. *australis* Holmberg
8. Legs yellowish except on last 1 or 2 tarsal joints, which are black; no black on second segment. Colombia. *huitaca* Banks
8. Legs yellowish except front femora and tibiae and bases of mid and hind femora which are black; black spot on second segment above; wings nearly evenly fumose. Ecuador. *quitus* Banks
9. Mid and hind femora rufous, remainder mostly black 10
9. If mid and hind femora rufous, rest of legs also 12
10. Mid and hind coxae and trochanters rufous; fore wings nearly evenly dark. Ecuador. *andicolus* Banks
10. Mid and hind coxae and trochanters black; wings hyaline with or without black bands 11
11. Wings hyaline but with two dark bands, one over the basal veins and the other over the marginal, cubital and third discoidal cells; abdomen entirely black; posterior border of pronotum very slightly angulate *jocaste* Banks
11. Wings hyaline (with brownish tint), without dark bands; tergites 1-6 on abdomen with the posterior border reddish; all of exposed tergite 7 is reddish; posterior border of pronotum transverse; all of fore femora (except

- knees), about basal half of midfemora and base of posterior femora dark; all tibiae and tarsi rufous. Brazil. *fuscus* n. sp.
12. Fore wings with 2 dark bands 13
12. Fore wing not banded or wholly dark 15
13. Strongly silvery sericeous on clypeus, face, mesopleura, a band across apex of propodeum, on sides of all tergites after the first, the dorsal sides of second, third and fifth tergites and across apex of fourth tergite; a few long conspicuous hairs in middle of posterior edge of sternites 2 through 6; last tergite strongly hairy. Peru *ornatus* n. sp.
13. No strong silvery pubescence (as glistening spots or streaks) as noted above, nor long hairs 14
14. Clypeus not 3× as broad above as long in middle; frontal groove distinct only below. Colombia, Brazil. *pretiosus* Fox
14. Clypeus 3× as broad as long, frontal groove complete. Colombia, Brazil, Ecuador. *machetes* Kohl
15. Fore wings without large black spot; hind margin of abdominal segments often rufous. Brazil. *marginatus* Banks
15. Fore wings with a large black spot 16
16. Legs all rufous except coxae, trochanters and last 4 tarsal joints; both pair wings all black. Argentina. *anthracinus* n. sp.
16. Legs not rufous as above; only fore wings black or with a black spot 17
17. Only the apical margin of wings hyaline, rest black. Ecuador. *orejones* Banks
17. Basal fourth of basal cell and behind it hyaline, rest black. Brazil. *nubilus* Fox

Males

1. At least the fore and mid femora partly rufous, or the legs largely pale yellowish to white; abdomen with basal 3 segments reddish or whitish, or the second segment and part of third rufous above and below; posterior border of pronotum white; last tergite white 2
1. Legs wholly black with tarsal joints sometimes dark brown; 3 basal segments of abdomen black or with sides of first and second slightly yellowish 4
2. All trochanters, femora and tarsi reddish, except the apex of posterior pair are dark at apex; first pair coxae black at base, reddish on apical half above with a white spot at apex above; last 2 pair coxae completely reddish; last joint fore tarsi black, first 4 joints yellowish, second pair tarsi with first 4 joints brown with yellow tips, last joint black; last pair tarsi all dark brown to black; fore spurs yellow, last 2 pair pure white; first 3 segments of abdomen reddish above and below, except most of dorsum of first segment, base of first segment and apex of third segment are blackish; wings clear hyaline; clypeus white with a black spot lengthwise in middle (0.2 of width). Brazil. (Fig. 5) *ruficrus* n. sp.
2. Legs pale yellowish to white, but posterior trochanters black, or only front and mid femora partly rufous 3
3. First, second and part of third segment of abdomen whitish, rest of abdomen black except for apical white spot; extreme base of first segment black; legs yellowish to white, hind trochanters black; clypeus and mandibles, except tip white; a white spot on lower lobe of pronotum just above fore coxae; last two tarsal joints of fore legs dark. British Guiana, Colombia. (Fig. 9) *modestus* Smith

3. Abdomen with first segment black (partly rufous below) second and part of third rufous above and below; legs mostly dark; front coxae pale yellowish at tips, front and mid femora rufous on apical half; front tibiae and tarsi (except last 2 joints) rufous; mid tibiae rufous on more than basal half, dark at tip, last 2 pair tarsi pale, tips of joints black, and last joint all black; hind legs almost entirely brown beyond the black coxae; tibial spurs whitish; no cloud in fore wing. Colombia. (Fig. 10) *rufigaster* Banks
4. A cloud over marginal cell extending backward across second and third cubital cells and into the discoidal cell; a very faint cloud over basal veins; clypeus almost all white, only a central triangular black spot, narrow at apex, the white spots covering about 0.8 preapical edge, and at the base the black spot occupies about 0.5 of width of clypeus; a narrow blackish, hairless rim across front of clypeus; genitalia characteristic; parameres scalloped on inner edge, with 3 transverse ridges, the apical 2 forming a U-shaped ridge; the tooth on middle of inside edge of volsellae obsolete; the outside surface of apex of volsellae with numerous small spines. Brazil. (Fig. 6) *unifascias* n. sp.
4. Wings almost hyaline or completely dark, no cloud; a narrow apical black hairless rim across front of clypeus 5
5. Wings hyaline slightly brownish; clypeus with a white spot each side covering 0.4 width of clypeus; posterior edge of pronotum with a white band; body and legs with a brownish tinge; a white ring around base of posterior tibiae; spurs white; genitalia characteristic; parameres very broad and with long hairs on all inside edge and over apical 0.25 of surface; volsellae with exceptionally large apex with blunt tip, the tooth on middle of inside very small; subgenital plate short and broad, rectangular. Brazil. (Fig. 7) *anomalus* n. sp.
5. Wings black; two white bands across the front of clypeus just back of narrow hairless rim, which do not quite touch in middle, covering about 0.25 of length of clypeus; pronotum completely coal black as is the whole body except the two white bands on clypeus; spurs black; subgenital plate characteristic; sides of basal half subparallel (slightly concave just above base), the plate becoming narrower from middle to the broad (about 0.3 as broad as base) apex, plate not rectangular as is the case in almost all other species; parameres not scalloped on outside; volsellae with a broad tooth in middle and with a very broad apex. Chile. (Fig. 8) *chilensis* n. sp.

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Growth of Green Algae with Myxomycete Plasmodia¹

WALDO R. LAZO²

ABSTRACT: Myxomycete plasmodia of several species, previously freed from bacterial contaminants, were grown on oat agar. To them were added pure cultures of 10 spp. of green algae. Three species of *Chlorella* were able to enter into full associations with *Physarum didermoides* and *Fuligo cinerea*, forming green plasmodia in which the algae multiplied in light.

Although many attempts have been made to grow myxomycete plasmodia when freed from bacteria, only a few have been successful (Cohen, 1939 and 1941; Hok, 1954; Sobels, 1950). Since 1958 I have successfully grown plasmodia under such conditions (Lazo, 1960). It has been demonstrated that most plasmodia grow slowly and with difficulty in this condition, although the plasmodium of *Physarum polycephalum* is a notable exception to this general rule. Since many plasmodia occur in nature in close association with algae, it was thought that algae might possibly serve the same purpose as do bacteria in 2-membered cultures.

MATERIAL AND METHODS

The plasmodia were grown on sterile oat agar consisting of oat flakes covered with non-nutrient agar to hold the flakes in place. They were freed from bacteria by various methods (antibiotics, low pH in the culture medium, migration). The sterility was thoroughly checked by seeding pieces of plasmodia in A-C Difco broth, brain-heart infusion, peptone-glucose broth, A-C agar, brain-heart agar. The plasmodia samples that were tested were taken, not from the advancing fronts of the plasmodia, which are almost always free from bacteria, but from immediately above the oats because this gives the best conditions for the growth of possible contaminants. The samples were seeded in the broth tubes and kept in the incubator at 25° C for ten days. Then, a sample of this broth was seeded in agar plates and again in broth tubes and kept in the incubator for an additional ten days.

The bacterium-free plasmodia were grown in pure 1.5 per cent agar and oats at a temperature of 25° C.

¹ This study was carried out at the Dept. of Biology of Princeton University and at the Dept. of Botany of the State University of Iowa. I wish to express my gratitude to Dr. J. T. Bonner, Dr. C. J. Alexopoulos, Dr. F. H. Johnson, Dr. Luigi Provasoli who kindly supplied me with the algae that I used in this experiment, Mr. O. R. Collins and Mr. J. Koevenig who kindly supplied me with the fruiting bodies of some of the Myxomycetes that I used and I especially acknowledge the invaluable counsel and help of Dr. G. W. Martin in the preparation of this manuscript.

This work was done on a Rockefeller Foundation fellowship, which is gratefully acknowledged, while on leave of absence from the University of Chile.

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The plasmodia used were those of *Physarum didermoides*, *P. polycephalum*, *P. gyrosum*, *Fuligo septica*, *F. cinerea*. Later some plasmodia were used that were contaminated with bacteria: *P. pusillum*, *P. compressum*, *Didymium iridis*, *D. squamulosum*, *D. minus*.

The algae used were *Euglena gracilis*, *Chlorella paramoecium*, *C. protothecoides*, *C. xanthella*, *C. saccharophyla*, *C. vulgaris* 259, *C. pyrenoidosa*, *C. luteo-viridis*, *C. zopfingiensis*, *C. ellipsoidea*, all in pure culture.

The plasmodia were seeded in the oat-agar plates and allowed to grow for three to five days. Then a small portion of each plasmodium was inoculated with one drop of the algal cells on the surface of the plasmodium. After inoculation the culture plates were placed in the incubator under fluorescent lamps at a constant temperature of 25° C.

RESULTS

The algae were incorporated in the bacterium-free plasmodia of *P. didermoides* and of *F. cinerea* in several trials, but were not successfully incorporated in those of any other species. All but one of the plasmodia which had not been freed from bacteria failed to incorporate the algae; the exception was *P. didermoides*. The bacterium-free plasmodia of *P. polycephalum*, *P. gyrosum* and *F. septica* appear to take the algal cells and digest them, but the plasmodia do not become green. On the other hand, after three or four days the white plasmodia of *P. didermoides* and *F. cinerea* appeared green in color and under a microscope the algal cells could be seen moving with the protoplasm within the plasmodial veins. Later, the algae were deposited in the walls of the veins and, with the walls, formed a green crust which, when the plasmodium became old and dried, usually cracked. The veins then appeared dry and white.

Summarizing these results, of the species of algae tested only three, *C. protothecoides*, *C. xanthella*, and *C. ellipsoidea*, were able to enter into full association with two species of myxomycetes tested, *P. didermoides* and *F. cinerea*. There was, in addition, some slight evidence of temporary association between these species and *C. saccharophyla* and *P. didermoides*, but it failed to persist.

Results were negative in all trials with *P. polycephalum*, *P. gyrosum*, *P. pusillum*, *P. compressum*, *F. septica*, *D. iridis*, *D. minus* and *D. squamulosum*.

If transfers are made from a green section of the plasmodium the new plasmodia will be green also. A green plasmodium may even be obtained from a white one, provided the white one has a few algal cells but an insufficient number to make it appear green at the time of the transfer. On the other hand, if a green plasmodium is kept in darkness, one part of it may become white if in the migration process that part loses all the algae.

The association plasmodium-algae grows much better than the plasmodium alone and is much more resistant to acidity than is the plasmodium in pure culture. *P. didermoides* and *F. cinerea* associated

with *C. protothecoides* or *C. xanthella* were able to grow in a medium buffered at pH 4.5 (McIlrairie, 1921). In both cases the plasmodia without algae grew only slightly or not at all at that pH.

Myxomycetes which have been purified from bacteria are rarely able to fruit. *Physarum polycephalum* is exceptional in this respect, as in many others. However, by the use of streptomycin I obtained a strain of *P. polycephalum* that never fruited unless it became contaminated. In the case of *F. cinerea* and *Chlorella*, fruiting can be obtained in about two or three weeks. The control plates do not fruit.

The bacterium-free plasmodia of *P. didermoides* do not fruit either associated with algae or alone.

The spores of *F. cinerea*, even when many appear abnormal, are viable; I have obtained plasmodia from them on a few occasions in bacterium-free condition. Algal cells were present.

DISCUSSION

It is premature to say that a symbiosis has been obtained. It does seem that some algae may function in the same way as do bacteria with some of the Myxomycetes, and in the case of *F. cinerea* they may help the fruiting process. It is not yet clear why the algae can grow on the membranes of some plasmodia and not on those of others.

Pinoy (1907) and Skupiński (1928) postulated that Myxomycetes could be considered as symbiotic organisms with bacteria. It is now clear that bacteria, at least, not only make possible the vegetative growth of the plasmodia, but even contribute to completion of the life cycle. The results here reported seem to demonstrate that some algae may replace bacteria, functioning in the same way.

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Fishes of Chincoteague and Sinepuxent Bays¹

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ABSTRACT: A comprehensive monthly trawl survey of Maryland and Virginia's Sinepuxent and Chincoteague Bays found 65 species of fishes within 40 families and 59 genera currently occupying these two seaside bays. Twenty-three species were new to the fauna which, since 1876, now totals 99 species. Various methods, beach seining, crab potting, hook and line fishing and wire oyster test trays, were employed to capture smaller species. An annotated list of species, as well as comments regarding seasonal population dynamics, size ranges, ecological requirements or preferences, are presented. Fish distributions, hydrographic conditions and invertebrates, mainly crabs, squids and *Aurelia* illustrate the predominant use of the southern inlet as an avenue of entry into these bays. The establishment of the newer northern inlet at Ocean City, Maryland, has had a profound influence on the hydrography of Sinepuxent Bay. This has resulted in extinction, entry or reduction of various fish species. Little use is made of the northern inlet as an avenue of entry into Chincoteague Bay. The fishes and crabs that do enter Sinepuxent Bay by way of the northern inlet are currently not found beyond the 5-8 mile southward influx of water from that inlet.

The permanent establishment of the present northern inlet to Chincoteague Bay, via Sinepuxent Bay, in 1933 (Md. Cons. Dept. 1933) along with the economic development of the Ocean City, Maryland area places a greater demand on the need for increased knowledge of the fishes of this area and the effects of these inlets on species abundance, presence or distribution. Although Giovanni da Verazzano accidentally sailed into Chincoteague Bay in 1524 (Covington, 1915), it was not until 1876 (Uhler and Lugger, 1876) that the first contribution of 12 species of fishes was collected from these waters (Fig. 1). Seven additions to this list of fishes were made by Lugger (1877, 1878) who sampled the southern inlet at Chincoteague, Virginia. Goode and Bean (1879) added two more species to the list. Fowler (1913-45) in a series of nine papers and sporadic surveys, primarily at Chincoteague and Franklin City, Virginia, and Ocean City, Maryland, listed 51 additional species to extend the total to 72 then known from Sinepuxent and Chincoteague Bays, Maryland and Virginia, and their inlets (Table III). Murphy (1960) recorded three commercial species in the early catch records of these bays. Arve (1960) trap netting in Chincoteague Bay, north of South Robin Marsh, recently added two species to the list of fishes known previous to 1959. Dillon (1960) notes the sport fishery and species about Ocean City, Maryland. No comprehensive study of the fishes or their distribution and seasonal abundance within the entire length of the bays has ever been attempted.

¹ Contribution No. 161, Maryland Department of Research and Education, Solomons, Maryland.

Acknowledgments.—It is a pleasure to acknowledge the generous assistance of the following people who helped in various ways toward successful completion of this project: Messrs. Fred Sieling and John Arve of the Chincoteague Bay Station of the Maryland Department of Research and Education for facilities, boat use and physical endurance beyond the call of duty; Mr. Thomas Carver, U. S. Fish and Wildlife Service Laboratory at Franklin City, Virginia, for use of the R. V. "Louise"; Mr. George Ward, for piloting the "Louise" and Messrs. Michael Castagne and George Griffith for specimen information around the Franklin City Laboratory and lower Chincoteague Bay region; Mr. N. Jester of the Pocomoke High School for use of his data concerning odd and rare specimens which he obtained from the lower bay area; Messrs. H. Schwartz and John Edgar of Antioch College, Ohio; Mr. C. Huckins of the Chesapeake Biological Laboratory; Mr. W. Meredith of Mt. St. Mary's College, Emmitsburg, Maryland, all of whom contributed field work; Dr. Ernest A. Lachner, Associate Curator Fishes, U. S. National Museum, for his critical review of the manuscript and suggestions regarding presentation and format; Messrs. G. F. Beaven, D. G. Cargo, H. J. Elser and J. R. Longwell of the Chesapeake Biological Staff for additional grammatical and constructional comments; and Mrs. G. Lankford for typing the final draft of this paper.

DESCRIPTION OF SINEPUXENT AND CHINCOTEAGUE BAYS

The study area of Sinepuxent and Chincoteague Bays is located in Worcester County, Maryland, and Accomack County, Virginia. The combined length of these continuous bays is some 28 miles and lies in a NE-SW direction between the latitudes $38^{\circ}20'$ - $37^{\circ}53'N$ and longitudes $75^{\circ}06'$ - $75^{\circ}27'W$. The bays are separated from the Atlantic Ocean by a narrow strip of land, Assateague Island (Fig. 1). One natural inlet, with several smaller inlets, exists at the southern end at Chincoteague, Virginia. A hurricane-cut inlet is maintained (since 1933) at the northern end at Ocean City, Maryland. The maximum width, about 5 miles, is in Chincoteague Bay near Public Landing, Maryland. The narrowest area, one-quarter

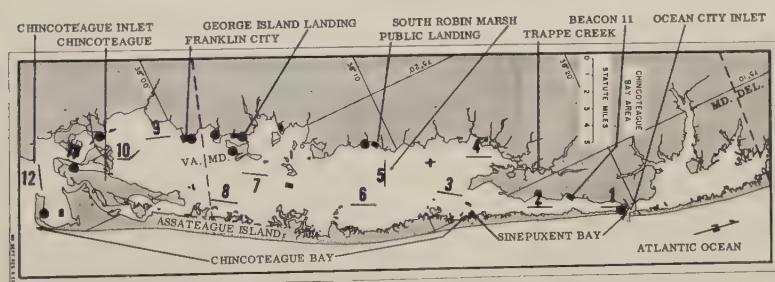


Fig. 1. Location of trawl (numbers), beach seine (dots), oyster tray (bars), and wire trap (cross) stations in Chincoteague and Sinepuxent Bays, Maryland and Virginia. 1. Beacon 4, Sinepuxent. 2. Beacon 17, Sinepuxent. 3. Beacon 35, Sinepuxent. 4. Newport Bay. 5. South Robin Marsh. 6. Foxhill levels. 7. White Rock. 8. Cedar Islands. 9. Franklin City. 10. Beacon 10, Virginia. 11. Beacon 7, Virginia. 12. Beacon 5, Virginia.

of a mile or less, exists in the 9 mile Sinepuxent Bay, the northernmost of the two bays. The watershed of the study area is 127.4 square miles while the area of the bay is 115.2 square miles (Bailey; personal letter; May 4, 1960). The largest freshwater tributary is Trappe Creek which enters the Newport-long Point area of the northern end of Chincoteague Bay. The average depth of both bays is 4 feet with the greatest depths of 25 and 50 feet occurring in channels at either inlet. The area is subject to constant wave action, particularly during the summer, for winds sweep freely over the adjoining dune or marsh shores. Turbidity is high. The shallowness permits abundant growths of bryozoans, *Ulva* and the red algae, *Agardhiella tenera*. Rainfall in the area amounts to about 48 inches per year (Sieling, 1960). The salinity patterns are well documented (McGary and Sieling, 1953, Md. Cons. Dept., 1934; Sieling, 1955, 1958; Sieling and McGary, 1952) and generally range from 13 to 30 o/oo (maximum 38 o/oo) at Public Landing, Maryland, and 22 to 36 o/oo at Franklin City, Virginia, with higher readings usually being noted at either inlet (Table I). Bottom salinities are approximately the same as surface salinities (Table II) throughout the area. Evaporation is highest during summer months (Pritchard, 1960). Tidal amplitude

TABLE I.—Surface and bottom salinities at 12 trawl stations, 1959, in Sinepuxent and Chincoteague bays

Station*		M O N T H							
		Apr	May	Jun.	Jul.	Aug	Sep.	Oct.	Dec.
1	S	30.2	29.8	31.1	31.8	31.2	30.8	29.7	30.8
	B		29.9	31.1	31.6	31.6	30.7	29.3	
2	S	30.7	28.8	30.4	31.5	31.2	30.8	29.5	27.1
	B		28.6	31.0	31.5	31.6	31.1	29.1	
3	S	26.0	26.4	30.4	33.2	25.6	29.8	28.6	27.3
	B		26.4	30.2	33.3	25.5	29.7	28.6	
4	S	24.6	24.0	26.7	30.2	22.7	27.3	28.1	
	B		24.0	28.5	30.2	22.9	27.1	28.0	
5	S	27.2	25.4	28.4	30.7	24.2	29.0	29.9	28.4
	B		25.9	28.4	31.1	24.7	28.9	29.9	
6	S	26.0	26.1	29.9	32.3	25.1	29.0	29.7	
	B		26.3	30.0	32.5	25.5	28.9	29.5	
7	S	28.1	26.9	32.0	33.7	29.3	31.1	30.3	28.8
	B		26.5	33.0	33.7	28.8	31.2	30.6	
8	S	28.4	28.9	32.3	33.8	28.2	30.4	30.6	
	B		28.6	33.2	33.7	28.8	31.2	30.6	
9	S	29.1	29.5	30.7	32.7	30.0	32.1	30.0	29.1
	B		28.8	31.1	32.3	30.2	31.8	30.3	
10	S	30.6	29.9	31.9	32.1	31.9	31.1	31.1	29.1
	B		29.9	32.7	32.0	31.8	31.2	31.4	
11	S	31.9	31.0	31.5	32.0	32.0	31.6	30.0	31.4
	B		31.2	31.6	31.8	32.0	31.6	30.6	
12	S	31.0	31.1	32.1	32.3	31.9	31.8	29.9	31.4
	B								

* As in Figure 1. S = Surface; B = Bottom.

at Ocean City averages about 3.5 feet and at the Chincoteague Inlet about 4.0 feet. Water temperatures average 25-27°C in the summer throughout the central portion of the study area and 23-24° at the inlets, which are influenced by oceanic waters (Table II). Pritchard (1960) estimates 9.3 days for 50 per cent of the water to be renewed while 62 days are needed for a 99 per cent water renewal. Short periods of complete ice cover and -1.7°C water temperatures have been recorded. The bottom types and locations are documented by

TABLE II.—Air, surface and bottom water temperatures at 12 trawl stations 1959, in Sinepuxent and Chincoteague bays

Sta- tions*		M O N T H							
		Apr	May	Jun.	Jul.	Aug	Sep.	Oct.	Dec.
1	S	6.0	17.4	20.2	26.5	20.3	28.0	14.0	8.0
	B		17.2	20.0	26.8	20.0	28.5	15.0	
	A		15.0		26.3	20.2	20.5	11.0	10.0
2	S	9.2	17.9		28.0	21.0	23.0	14.0	5.5
	B		17.4		28.0	21.0	23.0	15.0	
	A		17.9	**	26.8	21.0	22.0	10.0	7.0
3	S	10.4	20.0	**	26.7	24.0	23.5	14.0	6.0
	B		17.8	**	26.7	24.0	23.2	13.2	
	A		16.1	**	24.0	22.5	22.0	10.0	6.7
4	S	9.2	18.0	22.2	26.7	24.3	23.8	14.0	
	B		17.8	22.2	26.6	23.0	23.2	13.5	
	A		15.0	22.8	24.0	22.0	20.0	8.0	
5	S	9.4	17.8	21.9	25.8	26.9	24.0	12.5	6.3
	B		18.9	22.2	26.0	26.5	23.2	13.2	
	A		15.0	19.4	22.5	29.5	20.0	8.0	6.3
6	S	9.8	20.0		26.6	26.6	22.0	13.0	
	B		18.9		26.5	26.5	23.0	12.5	
	A		18.0		24.0	27.5	19.0	8.0	
7	S	10.6	17.9	22.0	27.3	26.5	21.0	12.0	6.2
	B		17.8	22.0	27.3	26.0	20.0	12.4	
	A		14.4	22.0	25.0	27.0	16.0	9.6	13.0
8	S	10.4	17.7	22.8	26.9	26.0	20.5	11.6	
	B		17.8	22.6	26.9	26.0	20.0	11.7	
	A		16.1	20.0	25.0	27.0	15.0	9.0	
9	S	11.0	18.9	23.3	25.0	25.4	22.1	12.1	14.9
	B		18.6	22.4	28.0	25.4	22.0	13.7	6.6
	A		16.7	22.8	29.0	24.0	22.1	14.5	
10	S	10.6	19.1	23.0	28.8	24.8	21.0	13.0	14.9
	B		19.1	23.2	28.3	24.6	21.0	12.6	6.6
	A			23.0	28.0	24.0	23.2	11.8	
11	S	9.8	18.7		26.0	23.7	22.4	12.7	7.6
	B		18.9		26.0	23.5	22.8	12.6	
	A				27.1	25.0	20.0	11.6	14.0
12	S	9.8	18.3		25.8	23.6	22.8	12.9	8.0
	B								
	A				25.3	24.0	22.5	11.4	12.0

* As in Figure 1. S = Surface; B = Bottom; A = Air; = No data;
 ** = Thermometer broken.

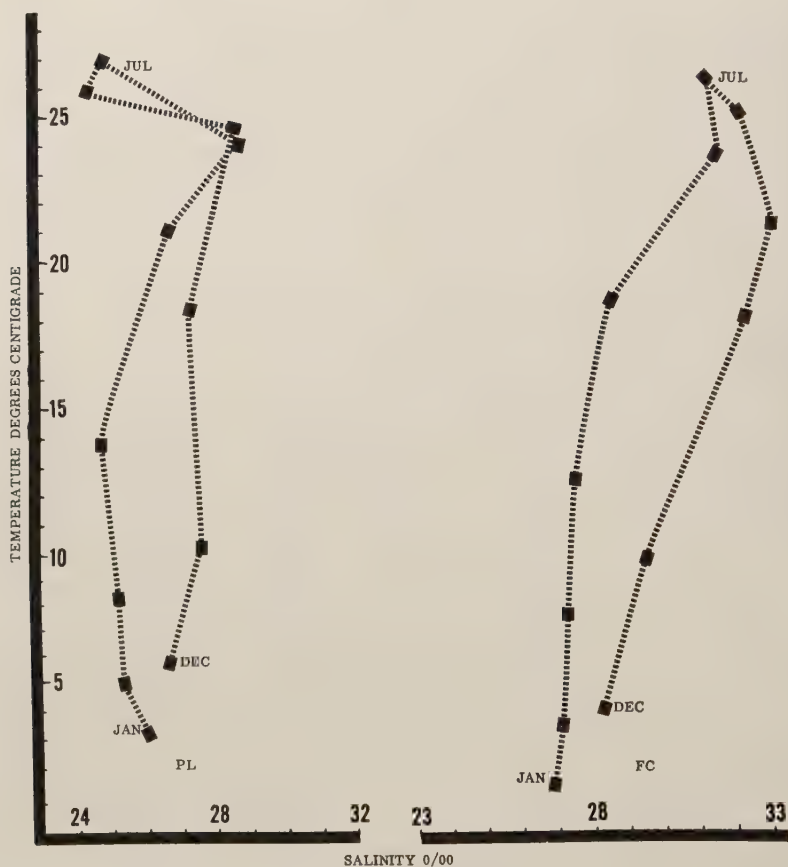


Fig. 2.—Hydroclimatographs for Public Landing (PL), Maryland and Franklin City (FC), Virginia.

U. S. Geological Survey (1937), Stout (1953) and Wells (1957). Generally sandy shoals exist on the eastern side of the bay while clay-mud bottoms predominate in the deeper western portion.

METHODS

Collections and records appearing herein were made during the period March 30 to December 16, 1959. Observations made between 1957-1960 from other localities are also included.

The primary collecting gear was a 25-foot otter trawl. Data from beach seining in the lower Virginia portion of Chincoteague Bay were obtained with a 50-foot, one-quarter-inch bag seine. Benthic species were captured in trays containing oysters which were set throughout the entire western length of Sinepuxent and Chincoteague Bays.

Seguin (1960) obtained data on young *Cynoscion regalis* with a small 15-foot tri-net off South Robin Marsh (Station 5). Verified specimens captured by hook and line have also been included.

Twelve monthly stations were established. The collecting effort at a station consisted of 15-minute tows (usually north to south) with the wind to facilitate easier boat handling. These tows in Sinepuxent Bay were along the channel which ran in a general north-south direction. The remaining stations were established on east-west lines five miles north of each other (Fig. 1). The latter stations encompassed deep channels and shoals over all types of bottoms. Some bias entered into the final placement of some of the easterly stations because of impenetrable shoals and boat draft, however, this was minimized as much as possible.

All specimens, unless stated otherwise, were measured to total length and released. Flounders, sharks and sea bass were tagged with monel strap tags on the left opercle to obtain data on their migratory patterns upon recapture.

To facilitate the presentation of localities a system of abbreviations was devised. The abbreviations used are OC for Ocean City, Maryland; PL for Public Landing, Maryland; GIL for George Island, Landing, Maryland; FC for Franklin City, Virginia; Ch for Chincoteague, Virginia; and Co for Cockle Creek, Virginia.

ANNOTATED LIST OF FISH SPECIES

Carchariidae — Sand Shark Family

1. *Carcharias taurus* Rafinesque. Sand shark.

Several sand sharks 500-750 mm (all measurements refer to total length unless specified otherwise) were captured at OC, FC, and Ch during the summer of 1959 on baited clam or peeler blue crab, *Callinectes sapidus*. Previously reported by Fowler (1927) at Ch.

Carcharhinidae — Requiem Shark Family

2. *Mustelus canis* (Mitchill). Smooth dogfish.

Two males, 900 and 1100 mm, were caught by hook and line at FC, July 29, 1958. Small specimens taken at Ch by Fowler (1913, 1927, 1930).

3. *Carcharhinus milberti* (Müller and Henle). Brown shark, Sandbar shark.

This species is only tentatively included for there are numerous sightings and reports of six-foot sharks within the bays. Sightings have been in Sinepuxent Bay (Station 6) and at Ch. Fowler captured small brown sharks at Ch (1927, 1930) and Co (1930).

Squalidae — Spiny Dogfish Family

4. *Squalus acanthias* Linnaeus. Spiny dogfish.

Four fish, two of each sex, males 800, 880 mm, females 755, 770 mm, were taken by trawl at Station 1 near OC on March 31,

1959. Undoubtedly this species ranges some distance from each inlet into the two bays proper; however, no others were captured or have been reported previously.

Rajidae — Skate Family

5. *Raja eglanteria* Bosc. Clearnose skate.

Eleven individuals, all from Station 12 were captured May 9, 1959; 2 males and 7 females (1000-1500 mm wide), June 1, one male (1180 mm wide), and October 1, one female (1360 mm wide). This species is present in oceanic shoal waters from May to November after which it moves into deeper waters outside of the bays. Apparently this species doesn't move far beyond the inlets into Chincoteague or Sinepuxent Bay proper. Several individuals have been taken by hook and line at the northern inlet. Two frayed egg cases were found floating near Foxhill Levels (Station 6). Clusters of egg cases of this species were brought up in the trawl as far south in Sinepuxent Bay as Station 2. *R. eglanteria* was previously reported abundant at Ch (Fowler, 1914, 1927, 1930) and Co (Fowler, 1914, 1927).

Dasyatidae — Stingray Family

6. *Dasyatis americana* Hildebrand and Schroeder. Southern stingray.

One female, 711 mm wide and weighing 50 pounds, was captured at FC, July 22, 1958, by Mr. Nelson Jester. Other specimens up to 3½ feet (1016 mm) wide have been sighted in Chincoteague Bay as far north as Foxhill Levels (Station 6) where they frequent the shallows and sandy bottoms on the eastern side. Occasionally a few large individuals are sighted in Sinepuxent Bay near Station 1. Arve (1960) reports one small specimen caught in a trap net just north of South Robin Marsh (Station 5).

7. *Gymnura micrura* (Bloch and Schneider). Smooth butterfly ray.

A pregnant female, 798 mm (31¾ inches) wide, with three male embryos, was captured at Station 12, September 17, 1959. The left uterus possessed one embryo (235 mm wide) while the right possessed two embryos (230 mm wide) whose snouts and wings were curved and folded inward on each other as noted by Radcliff (1916). These embryos are larger than the 5-6 inch specimens noted for a nearly full-term *micrura* (Radcliff, 1916; Smith, 1907) and a little larger than those noted by Bigelow and Schroeder (1953). Umbilical scars were obliterated. The lack of tail spine, large size and spotting around the edge of the wings of this specimen were distinct. These characters are within the size and range of variations noted by Bigelow and Schroeder (1953).

Myliobatidae — Eagle Ray Family

8. *Rhinoptera bonasus* (Mitchill). Cownose ray.

This species was not captured during the present survey, but

is present in Chincoteague Bay from June 2-October 15. It frequents the Chincoteague, Virginia area in large schools and is detested by the oyster planters of that area. This ray, up to 3 feet wide, is accused of the destruction of huge, if not entire, beds of oysters, seed oysters and clams. Many and varied devices are built around these beds but give little if any protection. It is my belief that the principal culprit is a dasyatid rather than *R. bonasus*. Cownose rays, locally called "bullfish," have been sighted as far north as Public Landing (near Station 5), Maryland. No cow-nosed rays seem to enter Sinepuxent Bay via the northern inlet.

Clupeidae — Herring Family

9. *Clupea harengus harengus* Linnaeus. Atlantic herring.

One 245 mm Atlantic herring was taken at Station 3 near South Point April 1, 1959. A short term anchor gill net fishery exists for this species between Stations 4-6. Apparently the Atlantic herring enter Chincoteague Bay during their northerly migrations and then exit, perhaps via the Ocean City inlet. Lugger (1877) noted large schools in Chincoteague Bay.

10. *Alosa sapidissima* (Wilson). American shad.

Although Fowler (1913) noted the presence of this fish in the pound nets around the lower inlet, only one 352 mm male shad was captured at Station 11, April 1, 1959. Some shad may stray into the Chincoteague, Virginia, inlet on their annual northerly spring migrations to spawn. None, however, have been recently known from the bay north of Station 11 where they contribute to the pound net fishery near Ch. Apparently, based on catch records for the period 1890-1908 (Murphy, 1960), sizable spawning runs utilized the fresher upper portions and bays above Ocean City prior to the opening of inlets which permitted salt water to enter the formerly fresh water areas. Few if any local spawning areas remain.

11. *Brevoortia tyrannus* (Latrobe). Atlantic menhaden.

Individuals varying in length from 48 to 107 mm of this pelagic species are common throughout Chincoteague Bay. Concentrated schools occur in June and July. Stations 4 and 5 consistently yielded samples. Fowler (1913, 1914, 1927, 1930) noted the abundance of menhaden about the southern inlet while Arve (1960) reports some caught in trap nets north of Station 5.

Engraulidae — Anchovy Family

12. *Anchoa mitchilli mitchilli* (Valenciennes). Bay anchovy.

The anchovy, 77-92 mm in length, is the most abundant summer species throughout Sinepuxent and Chincoteague Bays. Greatest concentrations of anchovies occurred in the vicinity of each inlet. This species was most common in both bays during October. Larval anchovies were common in the central portion of the study area around Stations 4-8 between April-May and October-December. Fowler (1913) observed some specimens on Assateague Island, apparently in an overflow tide pond.

13. *Anchoa hepsetus hepsetus* (Linnaeus). Striped anchovy.

The striped anchovy was found sporadically in Sinepuxent Bay, Stations 1-4, in August. Specimens varying in length from 77 to 137 mm were captured. Heavy external parasitization by a copepod, *Lerneaeenicus radiatus*, was common.

Synodontidae — Lizardfish Family

14. *Synodus foetens* (Linnaeus). Inshore lizardfish.

Four individuals, 77-98 mm, of this southern species were captured in August and September at Stations 10 and 11. High water temperatures and high salinities during this period most likely influenced its presence. A number of lizardfish were taken during 1957, 1959, and 1960 in Chesapeake Bay as far north as Chesapeake Beach, Maryland.

Anquillidae — Eel Family

15. *Anquilla rostrata* (LeSueur). American eel.

Three eels were captured in April, June and July at Stations 3, 4, and 5, respectively. This species frequents both bays until September as it is taken in crab pots during that period. Mr. N. Jester obtained a specimen from Co, June 30, 1958. Specimens are known from Ch (Fowler, 1914, 1927) and near Station 5 (Arve, 1960).

Belonidae — Needlefish Family

16. *Strongylura marina* (Walbaum). Atlantic needlefish.

One sight record of this species was obtained during the study period. The fish, about 16 inches long, were seen swimming along the surface of Chincoteague Bay, south of PL. Mr. M. Castagne captured a specimen 20¾ inches long at FC in 1958. Fowler (1913) reported this species at FC and OC (Fowler, 1919).

Cyprinodontidae — Killifish Family

17. *Cyprinodon variegatus* Lacépède. Sheepshead minnow.

Schools of 30-36 mm adults were captured along the PL beach. This species occurs along all beaches throughout the two bays. Fowler (1913) noted it at Ch as well as in Sinepuxent Bay (1918).

18. *Fundulus heteroclitus macrolepidotus* (Walbaum). Mummichog, Bull minnow.

The most common cyprinodontid throughout the bays. Huge schools are found along the beaches and especially around the docks at OC, PL, GIL, FC and Ch. Previously noted by Fowler (1913) at Ch, OC and in Sinepuxent Bay (1918).

19. *Fundulus luciae* (Baird). Spotfin killifish.

A single fish (56 mm) was seined near FC July 22, 1958, by Mr. N. Jester. Others have been seined north in Chincoteague Bay to Purnell Point. Fowler (1913) noted *luciae* in freshwater pools at Ch, but not in the bay proper.

20. *Fundulus majalis* (Walbaum). Striped killifish.

Large schools of this killifish inhabit the beaches throughout the southern portion of Chincoteague Bay south of GIL. Fowler (1913) recorded specimens at Ch and in Sinepuxent Bay (1918).

Gadidae — Cod Family

21. *Gadus morhua* Linnaeus. Atlantic cod.

Five- to seven-pound cod were caught in commercial fish pots from FC south during April 1-7, 1960. These were part of a large school of fish which remained inshore along Assateague Island all winter and contributed heavily to a gill net and hook and line sport fishery. None have been previously reported or caught in the bays. None are known to have entered via the northern inlet at OC.

22. *Merluccius bilinearis* (Mitchill). Silver hake, Whiting.

The whiting is found from September to May near the Chincoteague, Virginia, inlet. Schools of whittings occur offshore near the Ocean City inlet but they do not seem to enter Sinepuxent Bay via that inlet. The young (90-160 mm) enter Chincoteague Bay and move north to Long Point and Station 10 as stragglers. Adults were always found at Stations 11 and 12.

23. *Urophycis regius* (Walbaum). Spotted hake.

The spotted hake is present in the upper one-third of Chincoteague Bay, mainly between Stations 4-6, and Sinepuxent Bay, December to June as yearlings 68-92 mm and during April to June as 100-167 mm subadults. Small young may be found from May to November at Station 12 in the southern inlet. Larger specimens, above 170 mm standard length, are obtained outside the bays by the offshore trawlers. However, *U. chuss* is more common offshore than *regius* and the former constitutes a greater part of the trawl fishery catch (Murphy, 1960). *U. chuss* has yet to be found in either bay.

Syngnathidae — Pipefish Family

24. *Hippocampus erectus hudsonius* DeKay. Northern spotted seahorse.

Although not taken during the May, June or December samples, this subspecies (Briggs, 1958) is common along each inlet, especially at Stations 1-4 and 10-12. Specimens varying in total length from 58 to 150 mm were usually found clinging to the red algae *Agardhiella tenera* which abounds in the inlets and in the other portions of Chincoteague Bay. Uhler and Lugger (1876) noted seahorses in Sinepuxent Bay. Many are caught annually by tourists and trawlers in and around Ocean City and the offshore waters. Nomenclatorially Briggs (1958) is followed instead of Ginsburg (1937). Ginsburg (1937) did not apply the name of *erectus* (Perry, 1810), to this northern form.

25. *Syngnathus floridae* (Jordan and Gilbert). Dusky pipefish.

The first (118 mm) of two fish recorded from Chincoteague Bay was caught at White Rock (Station 7) while the other (125 mm) was taken at Beacon 10, Virginia (Station 10).

26. *Syngnathus fuscus* Storer. Northern pipefish.

The northern pipefish was found at all stations in October and between March and May. Individuals varied from 30-192 mm. This species was absent between Stations 4-9 during the period June to September.

Serranidae — Sea Bass Family

27. *Centropristes striatus* (Linnaeus). Black sea bass.

The black sea bass is common in Chincoteague Bay from April 1 to November 5, 1959. It is confined in Sinepuxent Bay to the inlet area near Station 1, rarely straying south to Station 4. Juvenile specimens, 30-37 mm standard length, predominate the April populations. By November these fish reach a standard length between 98 and 182 mm. In April and May black sea bass, locally called blackwill, are found at both inlets, Stations 1 and 12. Throughout the summer the schools continue to move northward and southward until they occupy Chincoteague Bay from Station 4 south and Sinepuxent Bay between Station 1 and Beacon 10, seldom occurring between Beacons 10 and 35. Populations were largest during the months of August, September and October. Many were caught during this period in traps and crab pots as well as in the trawl. Tagging failed to reveal definite migration patterns. Trawl sampling was a better means of observing population dynamics. During September there was a gradual outward movement of sea bass from the area and by November only an occasional specimen could be captured just north of PL. None were found in December. Fowler (1927) noted the sea bass abundance at Ch., while Arve (1960) trap netted 288 in 1958-1959 north of Station 5.

28. *Roccus americanus* (Gmelin). White perch.

White perch were not recorded during these observations, although they have been taken in crab pots or wire fish traps. Fish traps set in 1958 and 1959 by Arve (1960), over planted oyster shell beds near Station 4 and Newport Bay, captured 78 white perch. Murphy (1960) notes the previous importance of this species to the commercial fisheries of Chincoteague Bay where it often contributed up to 77,680 pounds to the fishery before the new northern inlet was formed. Today a few pounds are caught occasionally, usually only enough for private consumption. Fowler (1913, 1914, 1927, 1930) noted this species at OC, FC and Ch.

29. *Roccus saxatilis* (Walbaum). Striped bass.

An individual approximately 10 inches long was caught by hook and line at the Franklin City, Virginia pier while several others up to four pounds in weight were caught in Swan's Gut Creek. Local

fishermen did not know this fish in the study area nor has it been caught inside the inlet or mentioned in the literature. It does occur (December 1-9, 1959) just outside the Chincoteague, Virginia inlet and constitutes an excellent gill net and sport fishery in that area during some years.

Pomatomidae — Bluefish Family

30. *Pomatomus saltatrix* (Linnaeus). Bluefish.

Two young bluefish were trawled on July 8, 1959, at Station 10 (143 mm) and Station 11 (98 mm). Two hundred and thirty-two pounds of adult bluefish were captured by commercial stake gill nets at Foxhill Levels (Station 7) in September of 1959. Fifty pounds were taken by similar gear near Station 2 in Sinepuxent Bay. Arve (1960) captured some larger specimens in traps set near Station 4. Fowler (1913) noted small specimens at FC and Ch. Schools of bluefish from offshore apparently move in and out of the bays during the summer and fall months. Little else is known of their movements.

Carangidae — Jack Family

31. *Caranx crysos* (Mitchill). Blue runner.

The blue runner is common in Chincoteague Bay from Red Beacon 10 (Station 10) south during July and August. Specimens reaching 10 inches in length are often taken. Several were kept alive in May, 1958, at the U. S. Fish and Wildlife Laboratory, Franklin City, with perhaps a specimen of *C. hippos*. However, since the latter is missing, identification could not be verified and I have not placed it in this list.

32. *Selene vomer* (Linnaeus). Lookdown.

One specimen of this southern species was captured while beach seining in Watt's Bay in the summer of 1957. The lookdown was noted from these waters by Goode and Bean in 1879.

Pomadasyidae — Grunt Family

33. *Orthopristis chrysopterus* (Linnaeus). Pigfish.

The pigfish was found approximately from the Maryland-Virginia state line south in Chincoteague Bay and was especially common around piers. Specimens up to 7 inches long are found all summer. Fowler notes pigfish at OC (1913) and in the fall at Ch (1927).

Sciaenidae — Drum or Croaker Family

34. *Bairdiella chrysura* (Lacépède). Silver perch.

The silver perch occupies both bays from May to September with greatest concentrations occurring in August and September. Juveniles are found throughout the entire area and vary from 28 to 67 mm in standard length, the adults vary up to 168 mm. In May and June an occasional adult specimen can be found as far north in Chincoteague Bay as South Robin Marsh (Station 5). Silver perch

were previously noted in Chincoteague Bay at FC and Ch by Fowler (1913).

35. *Cynoscion regalis* (Bloch and Schneider). Gray trout, Weakfish.

Young trout occur in huge schools in August and September within Sinepuxent Bay south to White Rock (Station 7). Specimens 53-190 mm standard length occur in Chincoteague Bay from White Rock south in August. Trout occur from Cedar Island (Station 8) south in September. Occasional summer schools are found as far north in Chincoteague Bay as South Robin Marsh (Station 5, Seguin 1960). Trout do not move much further south than Station 2 (Beacon 17) in Sinepuxent Bay during the summer. One hundred and eleven pounds of adult trout were caught in September by commercial gill nets in Sinepuxent Bay. Fowler (1913; 1927) found trout at FC and Ch as well as at Co (1930). Fowler (1928) reports *C. nebulosus* from OC; however, this species was not taken during this survey.

36. *Leiostomus xanthurus* Lacépède. Spot.

The spot ranks second in abundance in Chincoteague Bay. It appears in June, is most abundant in June and July, and remains until late October. Large schools appear in Sinepuxent Bay and in the upper one-half of Chincoteague Bay from Stations 1-6. This population slowly shifts southward in August and September, until in September the northern edge of this population occurs only south of George Island Light (Va. Beacon 2). During this same period a few spot can be found in Sinepuxent Bay, a mile or so south of the northern inlet. Specimens taken during early summer were young-of-the-year or slightly older, while September and October specimens were adults which ranged to 190 mm standard length. Fifty-five pounds of spot were taken in September in Sinepuxent Bay by commercial gill net. Uhler and Lugger (1876) noted spot in Sinepuxent Bay while Fowler (1927, 1930) noted them from Chincoteague Bay in the fall. Arve (1960) captured 10 spot by trap netting north of Station 5.

37. *Menticirrhus saxatilis* (Bloch and Schneider). Northern kingfish, King-whiting.

This species is present August to September in the southern portion of Chincoteague Bay and around that inlet. Specimens were rarely found north of Station 10. In October kingfish, 108-198 mm, were found at inlet Stations 1, 11 and 12. Fowler (1913, 1927, 1930) noted their presence around Ch with the farthest northern record at FC (1913).

38. *Micropogon undulatus* (Linnaeus). Atlantic croaker.

The croaker was common in 1958 from Beacon 10 (Station 10) south in Chincoteague Bay during July to September. A few stragglers have been caught as far north in this bay as South Point.

Captured croakers are usually small, 150 mm; however, an occasional specimen of 350 mm is captured.

Sparidae — Porgy Family

39. *Archosargus probatocephalus* (Walbaum). Sheepshead.

Four sheepshead (180-250 mm) were caught by hook and line at the Franklin City pier in November, 1959.

40. *Lagodon rhomboides* (Linnaeus). Pinfish.

Although not captured during the present survey, this species frequents Chincoteague Bay during years of exceedingly high vegetation growth. Pinfish (Arve, 1960) were abundant in Chincoteague Bay in 1958 as far north as South Robin Marsh (Station 5). A slightly cooler year with less vegetative growth apparently kept this species out of the bay in 1959. Uhler and Lugger (1876) noted the pinfish in the Sinepuxent drainage area of Chincoteague Bay (which bay this was is uncertain, perhaps near Station 4). Fowler (1913) captured one specimen at Ch.

Ephippidae — Spadefish Family

41. *Chaetodipterus faber* (Broussonet). Atlantic spadefish.

A single fish (140 mm) was collected by beach seining in Watt's Bay in July, 1947, by Mr. M. Castagne of the Franklin City Laboratory. This species is a southern straggler that occasionally enters Chincoteague Bay.

Chaetodontidae — Butterflyfish Family

42. *Chaetodon ocellatus* Bloch. Spotfin butterflyfish.

Three specimens of this southern species were captured in Chincoteague Bay. One, 69 mm, was caught in a trap net three miles south of Station 4 by Arve (1960) on October 4, 1959. A 70 mm specimen was taken at Station 9 near FC by Mr. N. Jester, November, 1959, while a commercial crab fisherman captured an 80 mm specimen, November 12, 1959, near Piney Shoals in Chincoteague Bay.

Pomacentridae — Demoiselles

43. *Abudefduf saxatilis* (Linnaeus). Sergeant major.

The sergeant major is known from six specimens, 80-110 mm standard length, taken in Watt's Bay and near FC September 24, 1958.

Labridae — Wrasse Family

44. *Tautoga onitis* (Linnaeus). Tautog.

The tautog is very common at the Ocean City and Chincoteague inlets and at Station 1; occasionally south to Station 4. Especial preference is shown by this species for the rocky areas around the Ocean City inlet and in Isle of Wight Bay north of Ocean City, Maryland. Within Chincoteague Bay proper, a specimen 70 mm standard length was captured January 20, 1958. Several others were captured near Newport Bay (Station 4) in wire traps (Arve, 1960).

This species is usually taken by hook and line. None were captured by beach seine or crab pot. Fowler (1913) examined specimens from Ch.

45. *Tautogolabrus adspersus* (Walbaum). Cunner.

A 115 mm specimen was captured in a crab pot at Parnell Bay in Chincoteague Bay November, 1959. Undoubtedly, others occur, grazing near rocks or pilings where the trawl or crab pots were not operated.

Trichiuridae — Cutlass Fish Family

46. *Trichiurus lepturus* Linnaeus. Cutlass fish.

A single 500 mm specimen was caught by Mr. N. Jester in July, 1956, in Watt's Bay near Ch. This is a southern species which frequents the area as well as Chesapeake Bay during periods of high water temperatures and high salinities. Lugger (1877), Goode and Bean (1879), Fowler (1933) reported this species either at OC or at Ch.

Gobiidae — Goby Family

47. *Gobiosoma bosci* (Lacépède). Naked goby.

A common goby throughout the oyster bed area (Wells, 1958) of both bays which ranges roughly the length of the bays along the western shore. This diminutive species eluded trawl or traps, but was taken, usually in shallow water, in special oyster trays (5x18x41 inches) set over the length of the bay and during the entire year. This goby lives most of its life in or near empty oyster shell "boxes." Examination of these "boxes" usually produced individuals varying from 15 to 58 mm in length. Gobies are least active during the winter months from December to March, weathering out the cold waters usually one per shell. This species breeds during May to middle July. Contrary to Gunter (1945) this species was taken in salinities greater than 20 parts per thousand. Uhler and Lugger (1876) noted this species only in Sinepuxent Bay; however, they most likely overlooked it because of its shy and secretive nature. Fowler (1913B) found specimens of this species in the stomach contents of a merganser (*Mergus americanus*) at Ch.

48. *Gobiosoma ginsburgi* Hildebrand and Schroeder. Seaboard goby.

Two seaboard gobies, 48 and 51 mm, were taken in August and September at Station 9. *G. ginsburgi* prefers higher salinities than does *bosci* and thus will be found more often in that area of Chincoteague Bay from Franklin City southward or around the Ocean City inlet. Of the hundreds of gobies seen and captured by the oyster tray method (see comments under *G. bosci*), only two *ginsburgi* were found. These specimens were taken in 12 feet of water over a sand bottom and near oyster plantings which like *bosci*, it must also inhabit or utilize.

Triglidae — Searobin Family

49. *Prionotus carolinus* (Linnaeus). Northern searobin.

This species is present from May to September from Station 8 south. Most specimens, varying in length from 175-190 mm, were usually taken in the deep channel of the Chincoteague inlet. An occasional specimen is caught with hook and line on the Ocean City, Maryland inlet jetty. Fowler (1913) records this species from Ch.

Blenniidae — Blenny Family

50. *Chasmodes bosquianus* (Lacépède). Striped blenny.

The striped blenny is found associated with oyster shells throughout the two bays. Specimens 12-109 mm are common. Specimens larger than 25 mm can usually be obtained all year by a search of oyster "boxes." This species lays ovoid eggs attached to oyster shells in May and June. I have seen one 45 mm specimen caught on hook and line at the Ocean City inlet. Usually this method of capture is uncommon because of the striped blenny's size.

51. *Hypsoblennius hentzi* (LeSueur). Feather blenny.

Little is known of this rare Maryland blenny. Specimens (80 mm) were taken from Hardy's Hole (near George Island Landing) November 14, 1957, and Tom's Cove (southeast of Chincoteague, Virginia) September 14, 1959 (92 mm), and in oyster trays from the Maryland-Virginia state line southward. This blenny is apparently similar in habitat preference and habits to *G. bosci*, *G. ginsburgi* and *Chasmodes bosquianus*. *Hypsoblennius* associates with oysters in the more saline portion of Chincoteague Bay south of White Rock (Station 7) more often than does *Chasmodes*.

Stromateidae — Butterfish Family

52. *Poronotus tricanthus* (Peck). Butterfish.

Noted only in May and August by this survey, although the butterfish must occur commonly in the bays from May to October. Commercial gill net operations took 20 pounds at Foxhill Levels (Station 6) in September, 1959. Perhaps individuals or small schools from the offshore populations enter the bay for short periods. Uhler and Luger (1876) found butterfish in Sinepuxent Bay while Fowler (1913, 1927, 1930) noted their common presence at Ch. Arve (1960) cites the trap net capture of butterfish north of Station 5.

Mugilidae — Mullet Family

53. *Mugil cephalus* Linnaeus. Striped mullet.

Striped mullets (300-360 mm) were captured near FC and in commercial gill net operations (150 pounds in 1959) near Station 2 (Beacon 17 and vicinity). Murphy (1960) tabulates 366 pounds of mullet caught in 1958 with catches greater than 1000 pounds being made in the bays (?) between 1929-39. Where the latter were made is not known. Fowler (1913_B) found seven and one-half inch specimens of this species in the stomach of a merganser at Chincoteague, Virginia.

Atherinidae — Silversides Family

54. *Menidia menidia menidia* (Linnaeus). Atlantic silverside.

This abundant species, varying from 87 to 132 mm frequents Sinepuxent and Chincoteague Bays between October and June. The silverside apparently moves into other areas as it is absent in the bays during June to October, only one 50 mm specimen was taken in July. Fowler (1913) notes this species near Ch and OC (1945), while in 1913 and 1918 he found *M. beryllina* at (?) Assateague Island and in Sinepuxent Bay. The latter was not encountered during this survey nor has it been taken in beach samples in 1957 or 1958. *Menidia* sp. have been found in a merganser stomach at Ch. (Fowler, 1913_B).

Bothidae — Left Eye Flounder Family

55. *Paralichthys dentatus* (Linnaeus). Summer flounder.

The summer flounder, locally known as "fluke," is present over sandy bottoms from April through December with greatest concentrations adjacent to either inlet, May to July. A huge sport fishery exists at Stations 1, 2, 11 and 12 for this species. Specimens usually vary from 250 to 290 mm standard length with only an occasional large specimen taken at either inlet of up to 667 mm standard length. Flounders did not occupy the central portion of Chincoteague Bay until July when they were found throughout both bays. Trawling hampered by the dense beds of algae and bryozoans proved a poor method of sampling for this species. Traps or crab pots were more efficient means of capture as up to 16 could be caught in a Chincoteague Bay crab pot. Summer flounders utilize both inlets and begin to move out of the bays by August. The central portion of Chincoteague Bay is devoid of summer flounder by November. A residual population, however, can be found between Stations 1-5, apparently utilizing the last warm water areas of Chincoteague and Sinepuxent Bays (Table II). One summer flounder tagged at Station 4, August 28, 1959, was captured 312 days later, July 5, 1960, one mile south of the Ocean City Inlet for a net migration north of 10 miles.

56. *Scophthalmus aquosus* (Mitchill). Windowpane.

Small individuals, 80-90 mm, are found September to May in the inlets as well as from Station 1 south to Station 4 in Sinepuxent Bay. Adults over 230 mm are usually found over sandy bottoms near either inlet (Stations 1 and 12) from September to March. This species was captured by Fowler (1913) at FC and Ch.

Pleuronectidae — Righteye Flounder Family

57. *Pseudopleuronectes americanus* (Walbaum). Winter flounder.

Locally the winter flounder, called "black-back" or "halibut" is present throughout both bays from December to May especially in the deeper waters. Specimens, 243-318 mm standard length, are usually fat in December. Tagging failed to indicate any preference of pattern or movement. The inlet used most frequently as an avenue

of entry and dispersal is not known. Fowler (1913) found winter flounder at Ch.

Soleidae — Sole Family

58. *Trinectes maculatus maculatus* (Bloch and Schneider). Hogchoker.

This sole is present throughout the bays from August to October. Individuals commonly encountered measured 108-232 mm standard length. The hogchoker was expected in greater abundance, but was found only occasionally. No pattern of movement or area preference was evident.

Echeneidae — Remora Family

59. *Echeneis naucrates* Linnaeus. Sharksucker.

Numerous specimens 12-16 inches long were captured in May-September, 1958 and 1959 in commercial crab pots in Chincoteague Bay from approximately the Maryland-Virginia state line southward. Sharksuckers have been observed entering the bay attached to *Rhinoptera*, *Dasyatis*, *Mustelus* or *Squalus*.

Gobiesocidae — Clingfish Family

60. *Gobiesox strumosus* Peters. Skilletfish.

This diminutive species (12-67 mm) is present throughout both bays all year in association with oysters and *G. bosci*, *G. ginsburgi* and *C. bosquianus*. It spawns from late May through July. Normally it is found clinging to oysters or pilings in shallow water seldom over six feet deep. It spends its entire life in association with oysters.

Balistidae — Triggerfish and Filefish Family

61. *Alutera schoepfi* (Walbaum). Orange filefish.

Two individuals (210 mm) were taken at FC in July, 1959. Commercial crab fishermen south of Station 7 often catch this species. Fowler (1930) noted the orange filefish in the pound nets near Wallops Island just south of Chincoteague inlet.

62. *Balistes vetula* Linnaeus. Queen triggerfish.

Numerous specimens (160-250 mm) of this southern species were captured in commercial crab pots from approximately the Maryland-Virginia state line southward. One 160 mm specimen was captured on hook and line at FC.

Tetraodontidae — Puffer Family

63. *Sphaeroides maculatus* (Bloch and Schneider). Northern puffer.

The puffer, varying from 127 to 292 mm, is common May to October in the southern portion of Chincoteague Bay south of White Rock (Station 7), occasionally to Newport Bay (near Station 4) (Arve, 1960). It was extremely abundant at Stations 9 and 10 near FC. This species was found only at the deeper stations of Chincoteague and Sinepuxent Bays (Stations 2, 3, 4, 9 and 11) from August to October. Fowler (1913) found it at FC and Ch.

Diodontidae — Porcupine Fish Family

64. *Chilomycterus schoepfi* (Walbaum). Striped burrfish.

Three burrfish (105-127 mm) were captured September 2, 1959, at Stations 8 and 10. No young of this species were taken in the study area. Adults were captured in crab pots near Newport Bay (Station 4) in 1956. This species is apparently present throughout the lower Chincoteague Bay during the latter part of the summer and perhaps early fall.

Batrachoididae — Toadfish Family

65. *Opsanus tau* (Linnaeus). Oyster toadfish.

Collected from July to September; however, toadfish most likely frequent the bays all year. Individuals (98-223 mm) were taken at Stations 3, 5, 7, 9 and 10. Fowler (1927, 1930) found toadfish at Ch and Co.

DISCUSSION

Sixty-five species of 40 families and 59 genera were recorded within the limits of Chincoteague and Sinepuxent Bays during the present study. Specimens were captured mainly during trawling operations, but other data from 1957-59 beach seining, oyster trays and interested people have been incorporated.

Since 1876 a total of 99 species (Table III) have been recorded within some portion of Sinepuxent or Chincoteague Bays, primarily adjacent to each inlet or where the present northern inlet exists. Of the 65 species noted to currently occupy the area, 23 have not been previously reported.

TABLE III.—Species known to inhabit Sinepuxent and Chincoteague bays or their inlets

Species	A U T H O R I T Y						
	Uhler & Lugger	Lugger	Goode & Bean	Fowler	Murphy	Arve	Schwartz
<i>Carcharias taurus</i>	..	..	..	x	..	..	x
<i>Mustelus canis</i>	..	..	..	x	..	..	x
<i>Carcharinus milberti</i>	..	..	..	x	..	..	(x)
<i>Squalus acanthias</i>	..	..	..	..	..	..	x
<i>Raja eglanteria</i>	..	..	..	x	..	..	x
<i>Raja ocellata</i>	..	..	..	x	..	..	..
<i>Dasyatis americana</i>	..	..	..	..	..	x	x
<i>Dasyatis sayi</i>	..	..	..	x	..	..	..
<i>Gymnura micrura</i>	..	..	..	..	..	..	x
<i>Rhinoptera bonasus</i>	x	..	..	..	..	..	(x)
<i>Acipenser (sturio) oxyrhynchus</i>	..	..	..	x	..	..	..
<i>Megalops atlantica</i>	..	..	..	x	..	..	..
<i>Alosa mediocris</i>	..	..	..	x	..	..	..

TABLE III. (continued)

<i>Alosa pseudoharengus</i>	--	--	--	X	X	--	--
<i>Alosa sapidissima</i>	--	--	--	X	--	--	X
<i>Brevoortia tyrannus</i>	--	--	--	X	--	X	X
<i>Clupea harengus</i>	--	X	--	--	--	--	X
<i>Anchoa h. hepsetus</i>	--	--	--	--	--	--	X
<i>Anchoa m. mitchilli</i>	--	--	--	X	--	--	X
<i>Osmerus mordax</i>	--	X	--	--	--	--	--
<i>Esox niger</i>	--	--	--	--	X ?	--	--
<i>Synodus foetens</i>	--	--	--	--	--	--	X
<i>Bagre marinus</i>	X	--	--	--	--	--	--
<i>Ictalurus catus</i>	--	--	--	--	X ?	--	--
<i>Anquilla rostrata</i>	--	--	--	X	--	X	X
<i>Strongylura marina</i>	--	--	--	X	--	--	X
<i>Cyprinodon variegatus</i>	--	--	--	X	--	--	X
<i>Fundulus heteroclitus</i>							
<i>macrolepidotus</i>	--	--	--	X	--	--	X
<i>Fundulus luciae</i>	--	--	--	X	--	--	X
<i>Fundulus majalis</i>	--	--	--	X	--	--	X
<i>Lucania parva</i>	--	--	X	X	--	--	--
<i>Gambusia affinis</i>	--	--	--	X	--	--	--
<i>Gadus morhua</i>	--	--	--	--	--	--	X
<i>Merluccius bilinearis</i>	--	--	--	--	--	--	X
<i>Urophycis regius</i>	--	--	--	--	--	--	X
<i>Apeltes quadracus</i>	X	--	--	--	--	--	--
<i>Gasterosteus aculeatus</i>	--	X	--	X	--	--	--
<i>Fistularia tabacaria</i>	--	X	--	--	--	--	--
<i>Hippocampus erectus</i>	X	--	--	--	--	--	X
<i>Syngnathus floridae</i>	--	--	--	--	--	--	X
<i>Syngnathus fuscus</i>	--	--	--	X	--	--	X
<i>Centropristes striatus</i>	--	--	--	X	--	X	X
<i>Roccus americanus</i>	--	--	--	X	--	X	--
<i>Roccus saxatilis</i>	--	--	--	X	--	--	X
<i>Perca flavescens</i>	--	--	--	--	X	--	--
<i>Pomatomus saltatrix</i>	--	--	--	X	--	X	X
<i>Rachycentron canadum</i>	--	--	--	X	--	--	--
<i>Alectis crinitis</i>	--	X	--	--	--	--	--
<i>Caranx crysos</i>	--	X	X	--	--	--	X
<i>Selene vomer</i>	--	--	X	--	--	--	X
<i>Seriola (lalandi) dumerili</i>	--	--	--	X	--	--	--
<i>Vomer setipinnis</i>	X	--	--	--	--	--	--
<i>Orthopristis chrysopterus</i>	--	--	--	X	--	--	X
<i>Bairdiella chrysura</i>	--	--	--	X	--	--	X
<i>Cynoscion nebulosus</i>	--	--	--	X	--	--	--
<i>Cynoscion regalis</i>	--	--	--	X	--	--	X
<i>Larimus fasciatus</i>	X	--	--	--	--	--	--
<i>Leiostomus xanthurus</i>	X	--	--	X	--	--	X
<i>Menticirrhus americanus</i>	--	--	--	--	--	--	X
<i>Menticirrhus saxatilis</i>	--	--	--	X	--	--	X
<i>Micropogon undulatus</i>	X	--	--	X	--	--	X
<i>Pogonias cromis</i>	--	--	--	X	--	--	--
<i>Sciaenops ocellata</i>	--	--	--	X	--	--	--
<i>Archosargus probatocephalus</i>	--	--	--	--	--	--	X

TABLE III.—(continued)

<i>Lagodon rhomboides</i>	x	--	--	x	--	x	(x)
<i>Stenotomus chrysops</i>	--	--	--	x	--	--	--
<i>Chaetodipterus faber</i>	--	--	--	--	--	--	x
<i>Chaetodon ocellatus</i>	--	--	--	--	--	x	x
<i>Abudefduf saxatilis</i>	--	--	--	--	--	--	x
<i>Tautoga onitis</i>	--	--	--	x	--	x	x
<i>Tautogolabrus adspersus</i>	--	--	--	--	--	--	x
<i>Trichiurus lepturus</i>	--	x	x	x	--	--	x
<i>Sarda sarda</i>	--	--	--	x	--	--	--
<i>Scomberomorus maculatus</i>	--	--	--	x	--	--	--
<i>Gobiosoma bosci</i>	x	--	--	--	--	--	x
<i>Gobiosoma ginsburgi</i>	--	--	--	--	--	--	x
<i>Prionotus carolinus</i>	--	--	--	x	--	--	x
<i>Prionotus (strigatus) evolans</i>	--	--	--	x	--	--	--
<i>Astroscopeus guttatus</i>	--	--	--	x	--	--	--
<i>Chasmodes bosquianus</i>	--	--	--	--	--	--	x
<i>Hypsoblennius hentzi</i>	--	--	--	--	--	--	x
<i>Peprilus alepidotus</i>	x	--	--	--	--	--	x
<i>Poronotus triacanthus</i>	x	--	--	x	--	x	x
<i>Mugil cephalus</i>	--	--	--	--	--	--	x
<i>Mugil curema</i>	--	--	--	x	--	--	--
<i>Menidia b. beryllina</i>	--	--	--	x	--	--	--
<i>Menidia m. menidia</i>	--	--	--	x	--	--	x
<i>Etropus microstomus</i>	--	--	--	x	--	--	--
<i>Paralichthys dentatus</i>	--	--	--	x	--	x	x
<i>Scophthalmus aquosus</i>	--	--	--	x	--	--	x
<i>Pseudopleuronectes americanus</i>	--	--	--	x	--	--	x
<i>Trinectes m. maculatus</i>	--	--	--	x	--	--	x
<i>Gobiesox strumosus</i>	--	--	--	--	--	--	x
<i>Echeneis naucrates</i>	--	--	--	--	--	--	x
<i>Alutera schoepfi</i>	--	--	--	--	--	--	x
<i>Balistes vetula</i>	--	--	--	--	--	--	x
<i>Sphaeroides maculatus</i>	--	--	--	x	--	x	x
<i>Chilomycterus schoepfi</i>	--	--	--	--	--	--	x
<i>Opsanus tau</i>	--	--	--	x	--	x	x

(x) Tentatively included from sight record or captured in previous years but not during the period of study.

Species known from offshore waters along Assateague Island from Ocean City, Maryland, to Chincoteague, Virginia, but which have not currently been taken or known to enter these bays are: *Scomberomorus maculatus* (which supports a huge winter, December-February, drift gill net fishery 2-5 miles off Chincoteague, Virginia); *Stenotomus chrysops*; *Menticirrhus americanus* (April-May); *Raja erinacea* and *Raja ocellata* (comprising 50-70% of the industrial scrap fish industry off Ocean City, Maryland); *Cynoscion nebulosus* (present September-November); *Prionotus evolans* (another component of the June-August scrap fish industry); and *Rachycentron canadum*. Tarpon, *Megalops atlantica*, although noted by Fowler (1930) in the pound nets near Chincoteague, Virginia, have not authentically been taken from the bays. Specimens of tarpon up to 88 pounds in weight

have been caught recently with hook and line in Virginia seaside bays to the south of Chincoteague, Virginia.

The permanent opening of the northern inlet at Ocean City, Maryland in 1933 has produced a profound change in the fish fauna of Sinepuxent Bay which once had much lower salinities than those of today. Commercial records 1890-1958 compiled by Murphy (1960) indicate notable shifts in the populations which once inhabited Sinepuxent Bay and undoubtedly Chincoteague Bay of such species as: shad, *Alosa sapidissima* (commercial catch was 51,800 pounds); alewives, *Alosa pseudoharengus* (592,000 pounds); pike (most likely *Esox niger*, 54,025 pounds), yellow perch, *Perca flavescens* (72,000 pounds); white perch, *Roccus americanus* (77,680 pounds); and catfish (probably *Ictalurus catus*, 20,000 pounds). Pearson (1931) mentioned the effect of the periodic closing on such species as: *Micropogon undulatus*, *Cynoscion regalis*, *Leiostomus xanthurus* and *Pomatomus saltatrix*.

Seasonal water temperatures and, to a smaller degree, salinities are important factors influencing and limiting the distribution of species within the study areas. In general, these shallow bodies of water act as excellent nursery grounds for young of the spot (*Leiostomus xanthurus*), weakfish, (*Cynoscion regalis*), silver perch (*Bairdiella chrysura*), summer flounder (*Paralichthys dentatus*), anchovies (*Anchoa mitchilli*), black sea bass (*Centropristes striatus*) as well as a host of smaller sized species such as gobies, blennies, etc.

A constant oscillation of populations was found to exist in the two bays studied. Winter flounders and hogchokers moved in to occupy the area during winter months along with such forage species as silversides and anchovies. Gradually, spotted hakes and summer flounders moved into the area with a disappearance of winter flounders and silversides during the summer months that followed. Black sea bass populations overlapped each of the above shifts during the period April to November. Spot, by June, moved into the bays, in mass, to be later replaced, at least in the lower portion of Chincoteague Bay, by the weakfish, porcupine fish, swellfish and lizardfish. Occasional southern stragglers, namely the butterfly fish (*Chaetodon ocellatus*) appeared during periods of high salinities and water temperatures. The inlets were characteristically populated by sharks, rays, skates, tautog, summer flounder, kingfish and bluefish.

The influence of the older, natural southern inlet on the distribution patterns of fish within the bays is most pronounced. The influence of the newer permanent northern inlet today is effective, at most, only as far south in Sinepuxent Bay as Beacons 11 and 12 (5-8 miles). The influence of the various inlets can be vividly shown hydrographically (Pritchard, 1960) through the distribution of fishes and by means of the patterns and distribution of other organisms. High salinities are influential in limiting the distributions of the cancrid and portunid crabs [*Cancer irroratus* (Sieling, 1957) and *Ovalipes ocellatus*] to the inlets or at most to Stations 1, 2, 11 and 12. *Cragon*

septemspinosa, a crustacean, is abundant throughout the bays during the period October to May and its greatest numbers were recorded in the southern portion of Chincoteague Bay or around the inlets or areas of high salinity. It is replaced during June to August by *Paleomonetes vulgaris*. The crustacean *Chloridella empusa* was also found in August near Stations 8 to 9 in the southern part of Chincoteague Bay. It probably utilized the Chincoteague inlet to enter this area. Another crustacean *Libinia emarginata* taken from July to September was found only at Stations 1, 8, 9, 10, 11 and 12 or near the inlets, especially the southern. *Callinectes sapidus*, present throughout the entire bay, did not show greater abundance near either inlet. The importance of the southern inlet as an avenue of blue crab entrance into Chincoteague and/or Sinepuxent Bay was shown by Cargo (1954, 1959). A general southern migration of adult females of this crab persisted with little or no usage of the Ocean City inlet. The squid (*Lolliguncula brevis*) also responds to the influence of the various inlets. In April-May specimens 60-70 mm long are found throughout both bays except for Stations 5-9, greatest concentrations being at each inlet. In the summer it is found throughout the bays but with diminishing numbers near the center or Stations 5-7. Largest specimens (230 mm total length) occurred at each inlet. In the winter *Lolliguncula* is again most prevalent between Stations 1-2 and 9-12. The jellyfish (*Aurelia aurita*) was also found only in the high saline, southern portion of Chincoteague Bay from Cedar Islands (Station 8) southward. Its presence in that bay could only have been possible by utilization of the southern inlet. The limpet [*Diodora alternata* (Sieling, 1956)] invaded Chincoteague Bay via the southern inlet. Only the rock crab, *Cancer irrorata*, is known to have entered Chincoteague Bay via the northern inlet (Sieling, 1957).

CONCLUSIONS

Sixty-five species of fishes within 40 families and 59 genera currently are known to occur in Sinepuxent and Chincoteague Bays, 23 of which have never been previously reported. A total of 99 species are now known to have occurred since 1876.

These bays serve as excellent nursery grounds for a number of commercial species of fishes as well as some of lesser importance.

Fish distributions, hydrographic conditions and invertebrates, mainly crabs, squid and *Aurelia*, illustrate the predominant use of the southern inlet as an avenue of entry into the bays.

The cutting and establishment of the newer northern inlet at Ocean City, Maryland, has had a profound influence on the hydrography of Sinepuxent Bay. This has resulted in extinction, entry or redistributions of species. Periodic closure before the inlet's permanency often had the reverse effect on species abundance and distribution.

Little use today is made of the northern inlet as an avenue of entry by fishes into Chincoteague Bay. The fishes and other species,

namely sharks, flounders, tautog, lady crab and blue crab, that do enter Sinepuxent Bay by way of the Ocean City inlet are not usually found beyond the 5-8 mile southward influx of water from that northern entrance.

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Observations on Feeding Habits and Behavior of Grizzly Bears

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ABSTRACT: While engaged in a spawning-ground survey of salmon on the Nakina River, British Columbia, an excellent opportunity was afforded to study the feeding habits and behavior of several grizzly bears. The major food items and the manner in which they were obtained are discussed. Other behavior patterns such as territorialism and social hierarchy are likewise considered.

During the month of August 1959, observations were made by Alaska Department of Fish and Game biologists on the feeding habits and behavior of bears (*Ursus* sp.¹) on a 2-mile stretch of the Nakina River, a clear-water tributary of the Taku River. The Nakina is located in its entirety in British Columbia, while the Taku has its mouth about 30 miles south of Juneau, Alaska (Kerr, 1948). The Nakina is the major producer of an important stock of king salmon (*Oncorhynchus tshawytscha*), and the observations on bears were made in conjunction with a survey of salmon in this 2-mile stretch of water.

During the first two weeks of the study, abundant bear sign was evident, although only 1 or 2 bears were actually seen; these were sighted at a considerable distance from the camp. Then within 2 or 3 days, three bears took up residence in the vicinity of the camp and became quite imperturbable with respect to the survey party. These three were often encountered at extremely close range and fortunately paid little heed to the biologists. Besides these permanent "residents," 9 other bears were observed in the survey area, a few of these being seen fairly regularly while others were observed only once or twice. The individual bears were readily distinguished by obvious physical characters (size, color, etc.) as well as by behavioral peculiarities. The bears ranged in color from a light silvery-yellow through light and dark brown to a dark bluish-brown color. None of the bears was very large; an estimate of the weight of the largest was 600-700 pounds, with the more usual size about 500 pounds. All appeared to be in good condition.

FEEDING HABITS

Fish and berries were the major items of food eaten by bears during the study period, and in this respect feeding habits during the late summer were similar to those of the Kodiak Bear (Clark, 1957). King salmon and pink salmon (*Oncorhynchus gorbuscha*) were the major fish food; highbush cranberries (*Viburnum edule*)

¹ Information concerning the classification of the grizzly-brown bear group is inadequate to supply a specific name.

seemed to be the major plant material consumed. These findings were borne out by direct observation as well as by cursory examinations of droppings. When carcass surveys were made every other day (Table I), counted carcasses were slit lengthwise so that they would not be counted on subsequent days.

Only half-hearted attempts were made by the bears to capture live pre-spawned fish in good condition. In the few attempts in which we saw bears run and jump into a group of fish in a shallow riffle, they were never successful in catching one. For the most part they ate dead fish, although they would occasionally take a spawned-out fish which was still alive but not active enough to escape. In this respect, feeding habits of these grizzlies differed from those of bears along other river systems in Alaska, such as the Karluk River, where live fish are taken very frequently by brown bears (Shuman, 1950).

There did not seem to be any preference shown with respect to degree of decomposition of the dead fish eaten. A bear would travel along the river taking 1 or 2 bites from several fish and then suddenly take one into the brush and consume most or all of it. By the end of August the majority of the salmon had spawned and died, and most of the carcasses had floated downriver. Some of the dead fish, however, had lodged in the alders along the banks, among boulders, or in deep pools where the current was weak. These eventually became bloated and rose to the surface, where they were readily available to the bears. As a result, during the latter part of the survey period the bears utilized a greater percentage of carcasses which were in advanced stages of decomposition. Percentages were determined

TABLE I.—Percentage of king salmon carcasses fed upon by grizzly bears along a 2-mile stretch of the Nakina River, B.C., in 1959

Date	Total number of Carcasses counted	Percentage completely eaten ¹	Percentage partly eaten ²
Aug. 7	76	27.3	3.6
9	90	1.8	11.8
11	158	*	34.9
13	236	*	25.0
15	224	4.9	15.8
17	140	*	35.4
19	84	8.3	52.8
21	51	9.7	25.0
23	21	36.4	60.0

¹ Fish consumed to the point where they could not be sexed or measured.

² Fish with one or more bites that could be readily sexed and measured.

* Not recorded.

by recording, every other day during the month, the total number of carcasses available along the 2-mile stretch of water as well as the number of carcasses which had been eaten by bears.

King salmon carcasses were taken more frequently than pink salmon during the early part of the study period when the kings were much more abundant. Later in the month, the percentage of pinks utilized was slightly higher. Presumably this was because king carcasses were becoming less abundant towards the end of the month. When both species were available in large numbers, the bears seemed to prefer kings. In previous years, when red salmon (*Oncorhynchus nerka*) were more abundant, these fish were taken in proportionately greater numbers.

The percentage of carcasses eaten more or less in entirety, as well as the percentage which had one or two bites taken from them, increased gradually throughout the study period (Table I). Two obvious reasons for the increase are (1) that to maintain an equal intake of food material with decreasing numbers of fish, the bears would necessarily have to utilize a greater proportion of the total number of carcasses available as well as utilize a given carcass to a greater degree, and (2) that more individual bears were observed during the latter part of the survey.

BEHAVIOR

As previously mentioned, three bears comprised the "resident" group in the study area. At almost any time, at least one of them could be seen in the vicinity of the survey camp. Probably the main attraction here was a carcass weir built at the lower end of the 2-mile study area. This was a wire screen supported by tripods and extending across the entire width of the river. Carcasses of dead salmon floating downriver from above collected on this weir and were measured and sexed by the survey party twice a day. This accumulation of fish flesh was an ideal situation for the bears.

At times, bears other than the three residents would appear on the scene at the weir site. The strange bears were treated as intruders by the residents, and either the former or the residents would immediately panic and leave the scene; whether intruders or residents left depended upon the size of the intruding bears. The residents generally held their ground and forced strange bears to move out of the area; however, the sight of one non-resident bear, the largest seen in the area, would scatter the residents as soon as it made an appearance. The other animals seemed to be merely passing by and for the most part did not take advantage of the fish accumulated on the weir; at times strange bears even made wide detours of the weir to get from above to below it or vice versa. Whether this was due to intraspecific territorialism or to the presence of human scent at the weir site or to both is uncertain. An initial distrust of the weir was demonstrated by the resident bears, but this was rapidly dispelled and after a few days they even used it as a bridge to cross from one side of the river to the other or to the center section, where more carcasses

were collected. When the weir was removed after the survey was finished, one of the bears still came back to the site and appeared to be somewhat puzzled by its removal.

The three residents seemed to be quite tolerant of each other. Two were almost identical in appearance, being of the same size and color (silvery-yellow), and in fact were thought to be the same bear until they appeared together for the first time. From then on, their distinctive markings were quite obvious. The third member of the group was larger and darker in color than the other two, and was probably a year older. At least two of the three had been observed by Department biologists during similar spawning ground surveys in previous years. For the most part, a threatening attitude was taken by one of the bears only when one tried to maneuver a salmon carcass away from the other. Then they would face each other and growl or roar, sometimes keeping the noise up for several minutes, and make short, fierce charges. Once or twice during these encounters, the third bear would appear and make off with the fish while the other two continued their threat behavior. At times one of these three bears would come up unexpectedly and startle another one. Generally the startled bear would run off a short distance and then look around, see that the intruder was one of the other residents, and return to the activity which had been interrupted.

Two of the resident bears would often engage in play in the river, standing on their hind legs and cuffing each other, and then eventually go back to searching the pools and shores for dead fish. In one deep pool where carcasses collected in large numbers, they would swim around on the surface with the noses and eyes under water, apparently looking for carcasses. When a carcass was seen, it was brought to the surface with the hind feet, then transferred to the forepaws and eaten or discarded. Rarely one would submerge completely in retrieving a carcass.

There was no apparent social hierarchy displayed among the resident bears; no one bear in particular seemed to be dominant in the group.

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Observations on the Developmental Condition of Neonatal Birds¹

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ABSTRACT: The artificial incubation of eggs of about 100 species of wild birds was attempted. Egg and clutch weights, egg volumes, incubation periods, neonatal weights, interims between hatchings within clutches, number of days before hatching during which eggs float, and lengths of 6 of the long bones for neonates and adults are reported. Colors of natal down and of soft parts, especially of mouth linings, are given. Differences in extents of development at hatching are described, and some evolutionary postulates are discussed. This paper attempts to establish procedural standards under conditions that may allow for accurate and significant interspecific comparisons of incubation and neonatal condition independent of parental attentiveness and other environmental variables.

INTRODUCTION

The morphologic condition of development of hatching is used as an important criterion by ecologists and systematists in classifying birds (Daniel, 1957). An exhaustive search through North American museums in 1950 (Wetherbee, 1957), however, revealed that there were less than a dozen spirit specimens available that could confidently be called neonatal.

Terms like "precocial" and "altricial," "nidicolous" and "nidifugous," to indicate the extent of development at hatching have been generally used in ornithology, but critical examination reveals that the categories are oversimplifications and that there are actually a multitude of intermediate conditions. To re-examine this subject it was deemed necessary to have many specimens taken at the time of hatching.

Evans (1891, 1892) in Scotland and Heinroth (1908, 1922) in Germany hatched out many Old World species, but they did not carry on morphological work. Baldwin and Kendeigh (1932), Kendeigh (1940), and Graber (1955) investigated some parameters of artificial incubation of eggs of a few species of wild birds. Wetherbee (1958 and 1959) described the artificial incubation of more than 100 species of wild birds. In spite of the above-cited works, ornithologists generally have the erroneous belief that eggs of wild birds, especially of passerines, cannot be incubated artificially.

The lengths of "natural" incubation periods of birds' eggs have been recorded throughout history. A great deal of those data are untrustworthy as Nice (1953; 1954) has indicated in her exhaustive review of the subject. Unfortunately, however, even the information

¹ Portions of these data were submitted to the University of Connecticut in partial fulfillment of the requirements for the Ph.D. degree.

² Contribution of the Dept. of Poultry Science and Massachusetts Cooperative Wildlife Research Unit supported by the University of Massachusetts, Massachusetts Division of Fisheries and Game, U.S. Fish and Wildlife Service and Wildlife Management Institute.

that is trustworthy (Kendeigh, 1952) is of little comparative value because of the environmental variables that presumably modify embryonic development and the incubation behavior of the sitting bird. Lack and Lack (1951) have shown, for example, that the period in *Apus apus* fluctuates between 18.5 to 24.5 days in the wild. Much greater margins of variability are encountered in the literature on incubation periods for individual eggs than I found in my experience with artificial incubation. A standardized method of incubation is needed.

Weights of wild birds' eggs have been most frequently taken under field conditions in which only crude determinations can be made.

Volumes of wild birds' eggs have been most often calculated from linear measurements (Amadon, 1943). As the shapes of birds' eggs vary widely, such indirect determinations are usually subject to wide error. A more direct method of determining volumes is needed.

Comparative descriptions of neonates, especially of the song bird species, have been practically nonexistent. Wetherbee (1957) summarizes those few data that have been published and indicates the need for specimens taken at the moment of hatching.

Quantitative data on extent of ossification at hatching are nonexistent for wild birds. Length of skeletal elements as a criterion of development is advocated by Hammet (1926): "... bone growth in length is largely due to increase in cell number while growth in weight is largely due to increase in cell size and density. The former is less affected by systemic determinants: sex, weaning, puberty." Hammet's work was based on rats. Dunn (1928) found "weight of the body . . . is a less reliable guide to the final size of the fowl (than the linear measurement) since it is highly variable (the coefficients of variation for bone length in the fowl are from about 3.5 to 4.5 per cent; body weight from about 12.18 per cent). . . ." Beebe *et al.* (1917) found that bone growth in birds becomes retarded a few hours before hatching and remains so until at least 24 hours after hatching.

Materials and methods for arriving at the data summarized in Table I are fully described in a previous paper (Wetherbee, 1959). In brief, incubation was at 37.8° C and 64 per cent relative humidity under forced draft conditions. Neonatal specimens were preserved in formaldehyde and prepared by potassium hydroxide corrosion, alizarin staining and glycerin clearing (see Williams, 1941). Measurements were made by vernier calipers.

COLOR OF MOUTH LININGS

Many species of birds have bright colorations inside the mouth and on expanded flanges of the rictal region. The hue varies with the species from yellow to red, and the rictal flanges also vary widely in size. Ticehurst (1910) stated that the conspicuous coloration serves as a target for the parent's regurgitative feeding and may even stimulate such behavior on the part of the parent. Cavity-nesting species

TABLE I.—Tabulated summary of notes on the artificial incubation and on the reproductive biology of various bird species

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
Green Heron <i>Butorides virescens</i>	16.08	13.05		80.39		72±20
Black-crowned Night Heron <i>Nycticorax nycticorax</i>	35.95			107.9		
Mallard <i>Anas platyrhynchos</i>	64.55					
Wood Duck <i>Aix sponsa</i>	35.08	23.53		315.7		
Black Vulture <i>Coragyps atratus</i>	98.27	75.70		196.5		16±6
Broad-winged Hawk <i>Buteo platypterus</i>	40.60	29.63	39.17			
Sparrow Hawk <i>Falco sparverius</i>	14.93	11.84				
Ruffed Grouse <i>Bonasa umbellus</i>	16.03	13.24			534±8	
Bobwhite <i>Colinus virginianus</i>	10.23	7.52			559±7	
California Quail <i>Lophortyx californicus</i>	8.55	6.64			559±7	
Gambel's Quail <i>L. gambelii</i>	9.66	7.26			559±7	
Common Coturnix <i>Coturnix coturnix</i>	10.68	8.03			395±15	
Ring-necked Pheasant <i>Phasianus colchicus</i>	32.47	23.28	29.12		550±0	
Golden Pheasant <i>Chrysolophus pictus</i>		20.18			535±0	
Turkey <i>Meleagris gallopavo</i>	75.70					
Guinea Chicken <i>Numida meleagris</i>	41.23	22.50	33.57		644±6	
Red Jungle Fowl <i>Gallus gallus gallus</i>	37.54	26.01			504±0	
Chicken (Sil.-Col. r. b.) <i>G. gallus domesticus</i>	48.41	37.15	48.41			
Virginia Rail <i>Rallus limicola</i>	8.52	5.58				
Killdeer <i>Charadrius vociferus</i>	12.74	9.89		50.95		0±7
American Woodcock <i>Philohela minor</i>	15.55	13.10		46.63		

TABLE I.—(continued)

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
Herring Gull <i>Larus argentatus</i>		60.60				
Common Tern <i>Sterna hirundo</i>	18.86	12.09	19.29			
Rock Dove <i>Columba livia</i>	16.87	12.22			414±5	
Mourning Dove <i>Zenaidura macroura</i>	7.52	5.15		15.03		27±2
Domestic Parakeet <i>Melopsittacus undulatus</i>	2.39	1.67			405±4	
Ruby-th. Hummingbird <i>Archilochus colubris</i>						17±17
Belted Kingfisher <i>Megasceryle alcyon</i>		9.33				33±4
Yellow-shafted Flicker <i>Colaptes auratus</i>	7.21	4.80				7±5
Downy Woodpecker <i>Dendrocopus pubescens</i>	2.08	1.67		8.32		5±3
Eastern Kingbird <i>Tyrannus tyrannus</i>	3.97	2.43	3.27	10.10	366±7	0±5
Eastern Phoebe <i>Sayornis phoebe</i>	2.06	1.50	2.03	9.04	375±0	11±0
Horned Lark <i>Eremophila alpestris</i>	2.75	2.09	2.63			
Tree Swallow <i>Iridoprocne bicolor</i>	1.80	1.34	1.72		346±0	
Bank Swallow <i>Riparia riparia</i>	1.47	1.04	1.41	7.79		36±9
Rough-winged Swallow <i>Stelgidopteryx ruficollis</i>	1.84	1.29	1.77		367±4	
Barn Swallow <i>Hirundo rustica</i>	1.95	1.47	1.88		364±0	48±10
Cliff Swallow <i>Petrochelidon pyrrhonota</i>	2.14	1.62	2.07			
Blue Jay <i>Cyanocitta cristata</i>	6.47	4.99	6.16		406±0	
Common Crow <i>Corvus brachyrhynchos</i>	18.61		16.15			
Black-capped Chickadee <i>Parus atricapillus</i>	1.20	0.85	1.16			61±10
Carolina Chickadee <i>P. carolinensis</i>	1.04	0.79		4.96		0±10

TABLE I.—(continued)

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
White-breasted Nuthatch <i>Sitta carolinensis</i>	2.23	1.63	2.17		351 ± 5	
House Wren <i>Troglodytes aedon</i>	1.41	1.08	1.44		330 ± 5	
Bewick's Wren <i>Thryomanes bewickii</i>	1.36	1.11		9.78	350 ± 10	
Carolina Wren <i>Thryothorus ludovicianus</i>	2.73	2.09		13.64		
Mockingbird <i>Mimus polyglottos</i>	4.60	3.50			298 ± 9	
Catbird <i>Dumetella carolinensis</i>	3.87	2.85	3.74	15.43	317 ± 3	12 ± 5
Brown Thrasher <i>Toxostoma rufum</i>		4.70				
Robin <i>Turdus migratorius</i>	6.39	5.02	6.29	21.20	295 ± 1	43 ± 10
Wood Thrush <i>Holocichla mustelina</i>	5.26	3.46	5.17	14.90	335 ± 3	16 ± 6
Eastern Bluebird <i>Sialia sialis</i>	2.92	2.17	2.94	14.27	329 ± 6	
Blue-gray Gnatcatcher <i>Polioptila caerulea</i>	1.02	0.75		5.05	320 ± 6	
Loggerhead Shrike <i>Lanius ludovicianus</i>	4.56	3.33				
Starling <i>Sturnus vulgaris</i>	7.10	5.27	6.88	37.77		16 ± 5
White-eyed Vireo <i>Vireo griseus</i>	1.75	1.35			350 ± 7	
Red-eyed Vireo <i>V. olivaceus</i>	2.36	1.76	2.25			35 ± 9
Warbling Vireo <i>V. gilvus</i>	1.65	1.23	1.75			
Yellow Warbler <i>Dendroica petechia</i>	1.57	1.14	1.54	7.85	267 ± 2	
Chestnut-sided Warbler <i>D. pensylvanica</i>	1.41	0.97	1.41		264 ± 4	
Prairie Warbler <i>D. discolor</i>	1.38	0.98		5.51		
Ovenbird <i>Seiurus aurocapillus</i>	2.50	1.88	2.65	1.13		16 ± 0
Yellowthroat <i>Geothlypis trichas</i>	1.86	1.24	1.82		256 ± 12	22 ± 19

TABLE I.—(continued)

	Avg. egg wt.* (gms)	Avg. neonatal wt. (gms)	Avg. vol. (cc)	Avg. clutch wt. (gms)	Longest incu- bation (hrs)	Shortest hatch interim (hrs)
House Sparrow <i>Passer domesticus</i>	2.78	2.02	2.63	14.33	282 ± 3	10 ± 3
Red-winged Blackbird <i>Agelaius phoeniceus</i>	3.98	2.75	3.85	14.76	263 ± 1	23 ± 9
Common Grackle <i>Quiscalus quiscula</i>	6.76	4.96	6.57		310 ± 0	21 ± 0
Brown-headed Cowbird <i>Molothrus ater</i>	3.03	2.22	2.75		297 ± 6	
Scarlet Tanager <i>Piranga olivacea</i>	3.38	2.70	3.40			
Cardinal <i>Richmondia cardinalis</i>	4.27			12.62	298 ± 9	
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	3.94	3.10	4.07	16.92	294 ± 5	
Purple Finch <i>Carpodacus purpureus</i>	2.00		1.92			
Rufous-sided Towhee <i>Pipilo erythrophthalmus</i>	3.82	3.07				
Chipping Sparrow <i>Spizella passerina</i>	1.54	1.09	1.50		274 ± 10	22 ± 16
Field Sparrow <i>S. pusilla</i>	1.67	1.23	1.66	6.51		24 ± 8
Swamp Sparrow <i>Melospiza georgiana</i>	2.06	1.46		8.25		
Song Sparrow <i>M. melodia</i>	2.35					

* Not necessarily fresh eggs.

have brighter coloration of the mouth and wider flanges as an adaptation to the poor visibility of the parent in the dark chamber.

The black-billed cuckoo, catbird, horned lark, and blue-gray gnatcatcher were the only North American birds examined having actual markings superimposed on the bright mouth linings. I have seen African weaver finches among the Old World species in the spirit collection of the American Museum of Natural History that have the markings elaborately developed, being metallic in luster.

The variation in mouth colors are probably attributable to at least three different factors: (1) a horny yellow covering sheathing the bones of the bill; (2) a transitory red or orange coloring of the epidermis by pigments from the yolk, probably carotinoids; and (3)

differences in extent of the blood vascular bed. In the first category are the yellow mouths of the flycatchers, swallows, thrushes, wrens, titmouses, and starlings. Red coloration, often noticeable also in the skin of the body, is extremely well-developed in the red-winged blackbird and rose-breasted grosbeak. As these species feed on plant-eating insects rich in red carotinoids (Nester, Derby, and DeWitt, 1948), and since xanthophyll (lutein) is selectively deposited in the egg yolk (Peterson, Hughs, and Payne, 1939), it would seem logical to assume that the food of the parents determines the color of the hatchlings' mouths in these species.

Skin color of these species fades out a few days after hatching. Palmer and Kempster (1919) maintain that in chickens xanthophyll is excreted through the skin of the bird and is oxidized; egg laying replaces that excretory process later on. Nestling blackbirds and grosbeaks continue to feed on phytophagous insects; perhaps they do not concentrate so much xanthophyll as their ovulating mother. Virgin and Klusmann (Kline, Schultze, and Hart, 1932) have reported that the avian organism is able to convert xanthophyll into a provitamin or more probably into a growth vitamin (differing from carotene). The utilization versus excretion problem would seem to hold promise of solution by using the red-winged blackbird as an experimental animal.

The third of the factors determining mouth color, capillary vascularization of the mouth, is conspicuous in the sparrows. This vascularity may be adaptive for oxygen exchange in the nestling's mouth. This interpretation of mouth color is favored by reference to Daniel's (1957) contention that the early respiratory activity of "altricial" birds is relatively inefficient because of incomplete fusion of the parabronchi of the lungs.

The observation of Saunders (1956) that the neonatal cedar waxwing has violet-blue lines in the mouth should be further investigated. It is suggested that fruits eaten by the young may account for this character, for it did not come to my attention in artificially incubated neonates.

One is impressed by the applicability of Ticehurst's theory (*loc. cit.*) on rictal flanges and cavity-nesting when the neonatal Starling is examined. On the other hand, the neonatal mockingbird, hatched in an open nest, also has extremely large rictal flanges. The presence of flanges is so unevenly distributed among passerine families and among species having entirely different nesting habits that the functional significance of these structures should be re-examined.

WEIGHT OF EGGS IN RELATION TO CONDITIONS AT HATCHING

As the weight of an egg diminishes with age and incubation and as (for all practical purposes) a "fresh" egg does not exist in nature, it is necessary to use some other indication of egg size for purposes of drawing comparisons between species. Fortunately, sometime during incubation of all eggs, the air cell becomes large enough (by

utilization of stored food by the embryo) to cause the egg to have a specific gravity of unity, *i.e.*, neither sinks nor floats in water, which permits the calculation of volume. A comparison of egg volumes and neonatal weights in Table III shows that the chicks of the majority of the species weigh about 75 per cent of the egg (at sp.g. 1.0) weight. Variations from that norm might be considered to be adaptive in different species; great caution needs be exercised, however, in attributing simple functions. A chick heavy in proportion to the egg from which it came may require for its immediate postnatal life a store of resorbed but unassimilated yolk. All species examined, whether "precocial" or "altricial," had large amounts of such neonatal yolk. A chick could be proportionately heavy because of an evolutionary shortening of incubation period relative to body development or because of an evolutionary slowing down of body development relative to incubation period or to differences in weights of yolk constituents and to differences in metabolic efficiencies. The ecologic requirements of a thinner shell or a smaller supply of water in a humid environment might also be contributing factors.

The brown-headed cowbird with its proportionately heavy chick (81%) may be adapted to its socially parasitic hatching by an evolutionary shortening of incubation period or a large store of yolk.

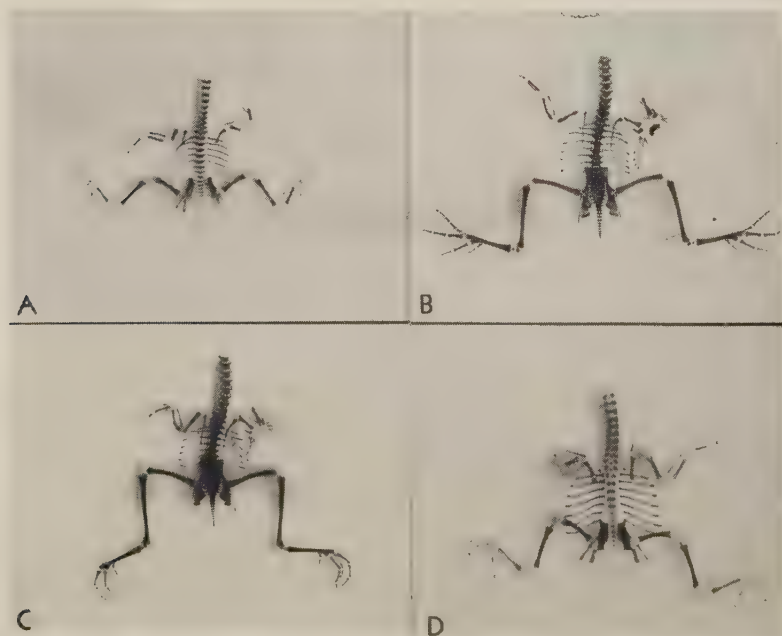


Fig. 1.—Comparison of ossification in neonatal birds. A. *Sialia sialis*, incubation period 13.5 days. B. *Coturnix coturnix*, 16.5 days. C. *Lophortyx californicus*, 23 days. D. *Cyanocitta cristata*, 17 days.

The blue jay (81% in Table III) has a slow body development relative to incubation period (compare Fig. 1 D with Fig. 1 A). The selective breeding that has brought about an increase in size of the chicken egg has only put more yolk in the neonate and has not lengthened the incubation period nor accelerated the body development. The incubation periods of both the domestic fowl and its supposed "ancestor," the red jungle fowl, are 21 days. Halbersleben and Mussehl (1921) found that chick (*Gallus*) weight was 64 per cent of egg weight regardless of differences in egg weight. At 35 days these weight differences had disappeared. My data for the eastern kingbird indicate that skeletal development was no more advanced in a neonate from an abnormally large egg than in neonates of that species hatched from normal-sized eggs.

The light relative weight (63%) of the common tern chick may be attributed to either the heavy shell or to lengthening of incubation period relative to rate of embryonic somatic development. Likewise the low value (67%) for wood thrush in Table III is correlated with a longer incubation period than that recorded for other turdids in Table I. The observed difficulty of yolk-sac resorption in this species may be related to that fact. The proportionate lightness of the four wood warblers, however, undoubtedly exemplifies an accelerated embryonic development that even their very short incubation period cannot counterbalance in restoring the 75 per cent norm. The bones of wood warblers are remarkably advanced in ossification at hatching.

INCUBATION PERIODS IN RELATION TO CONDITION AT HATCHING

The part that the length of incubation period plays in the condition of the young passerine bird at hatching has been mentioned above for the blue jay, which has a long (406-hour) period, and for the yellowthroat, which has a short (256-hour) period. Most other passerine species have periods between 280 and 370 hours (Table I), and their gross degree of ossification is much alike although certain bones vary from species to species. The yellowthroat, however, has a short (256-hour) period and a heavily ossified skeleton at hatching.

As the length of incubation period (Heinroth, 1908) is usually dismissed (erroneously) as the simple and proportional cause of differences in condition of young birds at hatching, it is perhaps appropriate to point to the common coturnix in Figure 1 B and to note that this exceedingly advanced neonate hatches in only 395 hours, 150 hours shorter than other species of quail which are less developed at hatching (Fig. 1 C).

Within the passerines the longer incubation periods produce the more helpless neonates, and the shorter periods produce the most advanced neonates. It can be summarized that a fast rate of embryonic development may shorten the incubation period but that a long incubation period does not produce a further advanced neonate.

INTERIMS BETWEEN HATCHING IN RELATION TO CONDITION OF NEONATES

At least 13 species listed in Table I start to incubate before the last egg in the clutch is laid, as indicated by the known interval of at least a day between hatchings. These include:

Green heron	Black-capped chickadee
Domestic parakeet	Robin
Mourning dove	Red-eyed vireo
Belted kingfisher	Ovenbird
Yellow-shafted flicker	Common grackle
Bank swallow	Red-winged blackbird
Barn swallow	

The hypothesis could be made that benefits accrue to the first hatched in a brood of several competing nestlings. If this were so, we ought to expect that the species listed above would have a strong selective pressure exerted upon them for early hatching. An examination of the neonates of these species supports the hypothesis, for it is among the 13 species that the least developed neonates are encountered. The red-eyed vireo is an exception.

When there is an ecological requirement for a species to hasten its reproductive period, it is surmised that the hen, through natural selection, becomes broody before the last egg is laid, or even immediately after the first egg is laid. This selective pressure on the behavior of the female then results in a new set of selective pressures among the offspring to hatch early because they no longer hatch synchronously. The ecological requirement for hasty reproduction then acts upon the behavior of the adult and is secondarily facilitated and abetted by the young becoming available earlier for direct evolutionary physical response to the ecological requirement. I can conceive that this chain reaction could be an important mechanism through which the altricial condition in birds arose and is sustained. The "semi-precocial" hawks and herons may either be in the process of acquiring a more "altricial" condition or more likely are unable to achieve such a complete altricity as passerines without the benefit of evolutionary feed-back via paedomorphosis of the adult.

BONE SIZE AT HATCHING IN RELATION TO BONE SIZE OF ADULT

The extent of development at hatching expressed as a fraction of the completed ossification of the adult is influenced by at least three factors that may or may not be interdependent: (1) the rate of somatic development of the embryo; (2) the length of the incubation period; (3) the magnitude of total ontogenetic distance that adulthood represents for that species.

For purposes of this discussion, the growth patterns of the species indicated in Table III (derived in part from basic data of Table II) will be compared and possible significances emphasized. Different

TABLE II.—Average length of neonatal (a) and mature (k) bones in millimeters

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	UL.
<i>Butorides</i>	a	2	10.3	12.6	6.8	3.8	7.6	8.1
<i>virescens</i>	k	2	48.8	80.5	42.8	36.5	67.3	75.0
<i>Nycticorax</i>	a	1	11.8	14.7	7.2	4.2	9.7	9.7
<i>nycticorax</i>	k	4	77.1	12.9	69.1	57.4	119.0	131.0
<i>Botaurus</i>	a	1	13.4	16.3	9.5	5.0	10.8	10.4
<i>lentiginosus</i>	k	3	78.7	129.0	63.4	56.3	108.0	122.0
<i>Aix sponsa</i>	a	2	13.6	24.6	10.2	6.0	9.6	7.8
	k	2	42.7	67.9	60.7	45.5	72.1	59.5
<i>Coragyps atratus</i>	a	1	21.0	27.9	12.4	5.5	14.5	15.0
	k	2	81.7	135.0	69.0	62.0	126.0	145.0
<i>Buteo lineatus</i>	a	1	11.4	13.7	7.2	3.4	10.4	10.4
	k	4	71.3	97.7	51.1	39.5	91.5	104.0
<i>B. platypterus</i>	a	1	12.8	14.9	7.5	3.8	11.0	11.0
	k	3	61.1	94.0	46.4	34.3	86.2	100.0
<i>Falco sparverius</i>	a	1	10.3	11.5	5.9	2.9	7.3	7.3
	k	3	36.2	48.8	28.4	24.2	44.8	47.6
<i>Bonasa umbellus</i>	a	1	14.7	20.4	10.5	5.7	9.0	8.5
	k	4	58.4	78.9	57.3	42.2	51.3	50.4
<i>Tympanuchus</i>	a	1	13.9	21.4	17.8	4.6	8.9	8.0
<i>cupido</i>	k	2	71.1	98.6	73.4	53.9	72.4	67.7
<i>Collinus</i>	a	2	11.8	17.0	8.6	4.5	6.0	5.4
<i>virginianus</i>	k	4	40.8	53.6	40.0	28.1	34.6	30.6
<i>Lophortyx</i>	a	1	11.8	17.3	8.7	4.7	6.3	5.1
<i>californicus</i>	k	3	40.7	55.9	40.9	28.4	33.2	28.8
<i>L. gambelii</i>	a	2	12.3	18.0	9.0	4.6	6.4	5.2
	k	2	40.7	56.0	41.5	27.9	33.4	29.9
<i>Coturnix coturnix</i>	a	1	11.4	15.4	9.0	4.8	6.4	5.3
	k	4	36.9	45.7	36.2	24.2	33.9	28.8
<i>Phasianus</i>	a	2	17.6	24.8	12.6	6.5	11.7	10.2
<i>colchicus</i>	k	4	80.6	109.0	74.2	53.2	73.5	66.9
<i>Gallus gallus</i>	a	2	17.5	23.6	12.8	7.2	10.6	10.0
	k	2	65.2	96.1	63.9	47.1	62.0	60.4
Chicken, Conn. (Sil.-Col. r. b.)	a	1	18.8	25.6	25.1	8.0	11.7	10.9
	k	4	101.0	146.0	93.0	69.0	90.0	88.0
<i>Rallus limicola</i>	a	1	11.4	16.9	7.8	3.0	6.9	5.5
	k	5	36.6	54.1	30.4	18.1	35.9	29.5
<i>Charadrius</i>	a	3	12.4	25.3	7.6	3.4	7.9	8.1
<i>vociferus</i>	k	3	26.5	52.1	29.0	18.5	39.1	44.1
<i>Philohela minor</i>	a	1	13.1	21.3	7.9	4.0	8.9	9.5
	k	5	37.7	54.7	37.8	25.8	43.9	48.6
<i>Larus argentatus</i>	a	1	17.0	35.0	13.2	5.0	15.8	15.9
	k	5	60.3	113.0	68.7	55.6	127.0	146.0
<i>Sterna hirundo</i>	a	2	10.8	17.2	8.6	3.6	9.0	9.8
	k	3	24.5	42.0	31.6	23.8	54.6	64.3

TABLE II.—(continued)

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	Ul.
<i>Columba livia</i>	a	2	8.2	9.4	4.4	3.2	5.2	6.4
	k	3	41.6	57.1	44.3	36.7	46.2	54.9
<i>Zenaidura macroura</i>	a	2	6.6	7.6	4.2	2.8	4.4	5.1
	k	4	28.8	38.6	33.7	25.8	32.6	38.0
<i>Melopsittacus undulatus</i>	a	2	4.2	4.8	2.2	1.6	2.5	2.2
	k	4	17.8	25.9	19.1	17.3	18.4	21.1
<i>Bubo virginianus</i>	a	1	13.7	16.1	7.8	4.2	12.9	12.8
	k	3	85.1	125.0	74.4	59.5	133.0	154.0
<i>Chordeiles minor</i>	a	1	8.2	11.3	5.8	3.2	5.8	6.8
	k	4	22.5	31.1	25.4	19.9	37.8	50.1
<i>Archilochus colubris</i>	a	1	2.5	2.6	1.2	0.8	0.56	0.64
	k	1	7.8	11.3	9.9	6.8	4.0	4.3
<i>Megasceryle alcyon</i>	a	2	9.8	11.4	5.2	3.6	7.0	8.0
	k	5	25.9	36.3	36.2	30.0	46.2	57.9
<i>Colaptes auratus</i>	a	2	4.8	5.6	1.7	1.2	2.9	3.0
	k	5	30.3	43.3	29.3	32.0	39.8	46.1
<i>Dendrocopus pubescens</i>	a	2	3.4	3.9	1.6	0.9	2.0	2.4
	k	5	16.4	25.4	14.8	18.1	22.2	26.6
<i>Tyrannus tyrannus</i>	a	2	4.4	5.6	3.0	1.9	3.1	3.8
	k	2	19.3	29.2	26.4	22.1	25.6	35.5
<i>Sayornis phoebe</i>	a	5	.35	4.6	2.9	1.7	2.6	3.2
	k	5	15.1	25.4	21.5	16.8	19.4	27.4
<i>Empidonax minimus</i>	a	1	2.8	3.9	2.5	1.4	1.9	2.6
	k	2	12.5	22.0	17.0	14.0	14.4	20.5
<i>Eremophila alpestris</i>	a	1	3.8	4.8	2.5	1.9	2.7	3.1
	k	2	20.1	33.4	25.3	20.9	24.9	29.4
<i>Iridoprocne bicolor</i>	a	5	2.7	3.7	1.9	1.5	1.6	2.3
	k	2	14.1	22.0	19.6	16.9	15.6	23.7
<i>Riparia riparia</i>	a	5	2.9	3.9	1.9	1.4	1.5	2.3
	k	3	12.4	19.7	16.3	14.5	12.9	19.8
<i>Stelgidopteryx ruficollis</i>	a	4	3.2	4.3	2.2	1.7	1.9	2.7
	k	1	13.0	20.8	18.3	16.0	15.9	24.8
<i>Hirundo rustica</i>	a	5	3.2	4.3	2.4	1.5	1.8	2.7
	k	2	13.1	21.0	19.3	15.6	15.5	23.7
<i>Petrochelidon pyrrhonota</i>	a	4	3.5	4.4	2.3	1.6	1.8	2.4
	k	2	14.0	23.0	20.0	17.3	16.0	24.5
<i>Cyanocitta cristata</i>	a	5	5.4	6.8	3.7	2.3	3.6	4.1
	k	5	32.1	52.4	30.7	26.5	32.7	38.0
<i>Corvus brachyrhynchos</i>	a	2	7.0	9.0	4.4	2.6	5.0	5.6
	k	5	51.5	87.9	50.6	44.3	66.8	81.0
<i>Parus atricapillus</i>	a	3	2.5	3.5	1.9	1.3	1.8	2.0
	k	4	12.9	23.8	13.9	13.3	14.2	18.1
<i>P. carolinensis</i>	a	3	2.6	3.9	1.9	1.2	1.8	2.0
	k	2	12.4	21.8	13.9	13.2	13.8	16.8
<i>Sitta carolinensis</i>	a	4	3.5	4.7	2.5	1.8	2.8	2.9
	k	5	15.9	25.5	17.5	16.4	19.1	24.3

TABLE II.—(continued)

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	Ul.
<i>Cinclus mexicanus</i>	a	1	3.6	5.1	2.8	1.9	2.6	2.9
	k	1	22.5	44.6	27.4	23.5	24.0	28.6
<i>Troglodytes aedon</i>	a	3	3.2	4.5	2.2	1.8	2.1	2.3
	k	4	14.5	23.1	14.1	13.1	13.6	14.2
<i>Thryomanes bewickii</i>	a	2	2.9	4.0	2.2	1.7	2.2	2.2
	k	3	13.7	23.5	13.6	13.0	14.1	15.7
<i>Thryothorus ludovicianus</i>	a	2	3.6	5.0	2.4	1.9	2.4	2.6
	k	4	17.3	29.1	16.7	16.2	16.7	17.7
<i>Mimus polyglottos</i>	a	3	4.9	6.4	3.3	2.2	3.2	3.7
	k	2	23.6	44.0	26.2	22.3	25.0	30.8
<i>Dumetella carolinensis</i>	a	5	4.2	5.9	3.1	2.0	2.9	3.3
	k	5	22.4	39.2	23.4	19.7	22.1	25.8
<i>Toxostoma rufum</i>	a	3	4.8	6.5	3.3	2.2	3.0	3.3
	k	5	27.9	48.1	28.2	24.1	27.4	30.1
<i>Turdus migratorius</i>	a	5	4.7	6.0	3.1	2.1	2.9	3.6
	k	5	27.3	46.0	31.3	26.6	28.8	35.4
<i>Hylocichla mustelina</i>	a	5	4.5	6.0	3.1	2.0	2.9	3.6
	k	5	23.6	41.6	25.6	22.8	23.9	29.1
<i>H. fuscescens</i>	a	1	4.0	5.5	3.0	1.8	2.7	3.2
	k	2	20.1	37.3	22.7	19.6	20.3	25.4
<i>Sialia sialis</i>	a	4	4.2	5.1	3.0	2.0	2.4	3.0
	k	3	17.6	30.0	32.3	19.2	20.4	27.5
<i>Polioptila caerulea</i>	a	5	2.6	3.9	2.1	1.5	1.8	2.2
	k	2	10.8	20.9	11.6	10.6	12.0	14.9
<i>Bombycilla cedrorum</i>	a	2	3.7	4.7	3.0	2.0	2.3	2.8
	k	5	18.7	28.3	24.4	20.1	20.3	25.2
<i>Lanius ludovicianus</i>	a	1	5.0	7.1	3.3	2.3	3.3	3.3
	k	2	23.1	38.6	24.7	22.2	24.2	29.5
<i>Sturnus vulgaris</i>	a	4	5.1	6.7	3.5	2.3	3.0	3.5
	k	4	25.1	43.3	30.5	26.2	27.5	32.5
<i>Vireo atricapilla</i>	a	1	2.9	4.2	2.3	1.9	2.4	2.7
	k	1	12.6	23.0	14.6	11.7	12.4	14.3
<i>V. griseus</i>	a	2	2.8	4.2	2.4	1.7	2.2	2.5
	k	2	14.1	25.7	15.6	13.6	14.9	17.8
<i>V. bellii</i>	a	1	2.7	4.0	2.0	1.4	1.9	2.3
	k	2	13.0	24.4	13.5	12.6	13.1	15.5
<i>V. olivaceus</i>	a	2	3.7	5.0	3.0	2.0	2.4	2.9
	k	5	15.9	26.5	19.3	16.9	17.5	22.2
<i>V. philadelphicus</i>	a	1	4.1	5.9	3.4	2.4	2.8	3.3
	k	1	14.2	24.0	15.1	14.5	15.0	19.0
<i>V. gilvus</i>	a	2	3.6	4.8	2.6	1.7	2.3	2.6
	k	2	13.8	24.5	16.5	14.8	15.3	19.7
<i>Mniotilta varia</i>	a	1	3.3	4.6	2.7	1.9	2.2	2.5
	k	5	13.3	23.7	14.7	13.7	14.5	18.5
<i>Dendroica petechia</i>	a	2	2.8	4.2	2.0	1.5	1.9	2.3
	k	3	14.1	25.6	15.2	13.4	13.8	17.3

TABLE II.—(continued)

Species	Stage	No.	Fe.	Tt.	Sc.	Co.	Hu.	Ul.
<i>D. discolor</i>	a	2	2.8	4.4	2.2	1.6	2.0	2.3
	k	2	12.1	24.0	12.3	11.7	12.8	15.9
<i>Seiurus aurocapillus</i>	a	2	3.4	5.3	2.7	1.9	2.5	3.0
	k	5	16.8	30.1	19.5	16.9	18.2	22.0
<i>Geothlypis trichas</i>	a	4	3.4	5.2	2.7	1.9	2.3	2.8
	k	5	14.3	26.7	14.3	13.1	13.3	15.2
<i>Icteria virens</i>	a	1	3.2	5.1	2.9	1.9	2.5	2.9
	k	3	20.3	35.6	19.6	17.8	19.3	21.5
<i>Passer domesticus</i>	a	5	3.9	5.0	2.5	2.0	2.4	2.6
	k	5	18.2	29.1	22.1	18.8	18.7	20.9
<i>Agelaius phoeniceus</i>	a	4	4.0	5.6	2.8	2.0	2.9	3.2
	k	4	24.5	40.3	28.2	24.8	27.2	32.3
<i>Icterus galbula</i>	a	1	4.6	6.1	3.4	2.2	3.0	3.7
	k	5	20.7	34.9	23.1	20.5	21.8	27.0
<i>Quiscalus quiscula</i>	a	5	5.0	6.7	3.6	2.4	3.5	4.0
	k	5	31.8	51.4	35.2	30.5	33.1	38.2
<i>Molothrus ater</i>	a	5	4.1	5.7	3.0	2.0	2.8	3.2
	k	5	20.9	35.5	25.7	22.9	23.5	27.8
<i>Piranga olivacea</i>	a	1	3.9	5.4	3.0	2.1	2.9	3.2
	k	5	18.1	29.1	21.6	19.0	20.5	25.9
<i>Richmondia cardinalis</i>	a	1	4.4	6.1	3.2	2.2	3.1	3.2
	k	5	21.6	36.4	23.3	20.6	22.5	26.5
<i>Pheucticus ludovicianus</i>	a	3	4.5	5.9	3.4	2.0	2.9	3.6
	k	5	21.9	34.7	25.2	22.0	23.5	28.6
<i>Pipilo erythrophthalmus</i>	a	1	4.4	6.1	2.5	2.0	2.9	3.4
	k	4	23.3	38.7	23.3	20.2	22.5	23.9
<i>Spizella passerina</i>	a	3	3.1	4.2	2.4	1.6	2.2	2.6
	k	3	13.5	22.5	16.3	14.0	15.7	19.1
<i>S. pusilla</i>	a	3	3.4	4.9	2.3	1.7	2.2	2.6
	k	3	15.1	25.2	16.7	14.5	15.9	18.3
<i>Melospiza georgiana</i>	a	2	3.6	5.1	2.2	1.9	2.2	2.4
	k	3	17.6	30.0	16.4	14.5	16.1	16.1
<i>M. melodia</i>	a	1	3.3	4.8	2.4	1.7	2.3	2.4
	k	4	18.2	30.5	17.6	16.6	17.8	18.3

bones of any species have different degrees of linear maturation. Thus the femur of the killdeer is 47 per cent developed at hatching while its ulner is only 18 per cent developed. The ulna of the Virginia rail, another "precocial" bird, is 19 per cent developed, comparable with that of the killdeer, but its femur is only 31 per cent developed. Natural selection operates differentially on developmental rates of individual characters in addition to the developmental rates of the whole organism. It therefore would be more accurate to speak of a precocial character rather than of a precocious bird.

It is immediately obvious that the terms "precocial" and "altricial,"

TABLE III.—Average neonatal weight¹ and neonatal bone size²

Species	Avg. wt.	Avg. bone size						Avg.
		Fe.	Tt.	Sc.	Co.	Hu.	Ul.	
<i>Butorides virescens</i>		21	16	16	10	11	11	14
<i>Nycticorax nycticorax</i>		15	11	10	7	8	7	10
<i>Botaurus lentiginosus</i>		17	13	15	9	10	8	12
<i>Aix sponsa</i>		32	36	17	13	13	13	21
<i>Coragyps atratus</i>		26	21	18	9	12	10	16
<i>Buteo lineatus</i>		16	14	14	9	11	10	12
<i>B. platypterus</i>	.75	21	16	16	11	13	11	15
<i>Falco sparverius</i>		28	24	21	12	16	15	19
<i>Bonasa umbellus</i>		25	26	18	14	18	17	20
<i>Tympanuchus cupido</i>		20	22	24	8	12	12	16
<i>Colinus virginianus</i>		29	32	22	16	17	18	22
<i>Lophortyx californicus</i>		29	31	21	16	19	18	22
<i>L. gambelii</i>		30	32	22	16	19	17	23
<i>Coturnix coturnix</i>		31	34	25	20	19	18	25
<i>Phasianus colchicus</i>	.80	22	23	17	12	16	15	18
<i>Gallus gallus gallus</i>		27	24	20	15	17	16	20
<i>G. gallus domesticus</i>	.77	19	18	27	12	13	12	17
<i>Rallus limicola</i>		31	31	26	16	19	19	24
<i>Charadrius vociferus</i>		47	48	26	18	20	18	30
<i>Philohela minor</i>		35	39	21	16	20	20	25
<i>Larus argentatus</i>		28	31	19	9	12	11	18
<i>Sterna hirundo</i>	.63	44	41	27	15	16	15	26
<i>Columba livia</i>		20	16	10	8	11	12	13
<i>Zenaidura macroura</i>		23	20	12	11	13	13	18
<i>Melopsittacus undulatus</i>		24	18	12	9	14	10	15
<i>Bubo virginianus</i>		16	13	10	7	10	8	11
<i>Chordeiles minor</i>		36	36	23	16	15	14	23
<i>Archilochus colubris</i>		32	23	12	12	14	15	18
<i>Megasceryle alcyon</i>		38	31	14	12	15	14	21
<i>Colaptes auratus</i>		16	13	6	4	7	6	9
<i>Dendrocopus pubescens</i>		21	15	11	5	9	9	12
<i>Tyrannus tyrannus</i>	.74	22.7	19.1	11.3	8.5	12.1	10.7	14.1
<i>Sayornis phoebe</i>	.74	23.1	18.1	13.4	10.1	13.4	11.6	15.0
<i>Empidonax minimus</i>		22.4	17.7	14.7	10.0	13.1	12.6	15.1
<i>Eremophila alpestris</i>	.79	18.9	14.3	9.8	9.0	10.8	10.5	12.2
<i>Iridoprocne bicolor</i>	.78	19.1	16.8	9.6	8.8	10.2	9.7	12.4
<i>Riparia riparia</i>	.74	23.3	19.7	11.6	9.6	11.6	11.6	14.6
<i>Stelgidopteryx ruficollis</i>	.73	24.6	20.6	12.0	10.6	11.9	10.8	15.1
<i>Hirundo rustica</i>	.78	24.4	20.4	12.4	9.6	11.6	11.3	15.0
<i>Petrochelidon pyrrhonota</i>	.79	25.0	19.1	11.5	9.2	11.2	9.7	14.3

TABLE III.—(continued)

Species	Avg. wt.	Fe.	Tt.	Avg. bone size			Ul.	Avg.
				Sc.	Co.	Hu.		
<i>Cyanocitta cristata</i>	.81	16.8	12.9	12.0	8.6	11.0	10.7	12.0
<i>Corvus brachyrhynchos</i>		13.5	10.2	8.6	5.8	7.4	6.9	8.7
<i>Parus atricapillus</i>	.73	19.3	14.7	13.6	9.7	12.6	11.0	13.5
<i>P. carolinensis</i>		20.9	17.8	13.6	9.0	13.0	11.9	14.4
<i>Sitta carolinensis</i>	.75	22.0	18.4	14.2	10.9	14.6	11.9	18.0
<i>Cinclus mexicanus</i>		16.0	11.4	10.2	8.0	10.8	10.1	11.1
<i>Troglodytes aedon</i>	.75	22.0	19.4	15.6	13.7	15.4	16.1	17.0
<i>Thryomanes bewickii</i>		21.1	17.0	16.1	13.0	15.6	14.0	16.1
<i>Thryothorus ludovicianus</i>		20.8	17.1	14.3	11.7	14.3	14.6	15.5
<i>Mimus polyglottos</i>	.76	20.7	14.5	12.5	9.8	12.8	12.0	13.7
<i>Dumetella carolinensis</i>		18.7	15.0	13.2	10.1	13.1	12.7	13.8
<i>Toxostoma rufum</i>		17.2	13.5	11.7	9.1	10.9	10.9	12.2
<i>Turdus migratorius</i>	.79	17.2	13.0	9.9	7.8	10.0	10.1	13.3
<i>Hylocichla mustelina</i>	.67	19.0	14.4	12.1	8.7	12.1	12.3	13.1
<i>H. fuscescens</i>		19.9	14.7	13.2	9.1	13.3	12.5	13.8
<i>Sialia sialis</i>	.74	23.8	17.0	9.2	10.4	11.7	10.9	13.8
<i>Polioptila caerulea</i>		24.0	18.6	18.1	14.1	15.0	14.7	17.4
<i>Bombycilla cedrorum</i>		19.7	16.6	12.2	9.9	11.3	11.1	13.5
<i>Lanius ludovicianus</i>		21.6	18.3	13.3	10.3	13.6	11.1	14.7
<i>Sturnus vulgaris</i>	.77	20.3	15.4	11.4	8.7	10.9	10.7	12.9
<i>Vireo atricapilla</i>		23.0	18.2	15.7	16.2	19.3	18.8	18.5
<i>V. griseus</i>		19.8	16.3	15.3	12.5	14.7	14.0	15.4
<i>V. bellii</i>		20.7	16.3	14.8	11.1	14.5	14.8	15.4
<i>V. olivaceus</i>	.78	23.2	18.8	15.5	11.8	13.7	13.0	19.0
<i>V. philadelphicus</i>		28.8	24.5	22.5	16.5	18.6	17.3	21.4
<i>V. gilvus</i>	.70	26.0	19.5	15.7	11.4	15.0	13.1	16.8
<i>Mniotilta varia</i>		24.8	19.4	18.3	13.8	15.1	13.5	17.5
<i>Dendroica petechia</i>	.73	19.8	16.4	13.1	11.1	13.7	13.2	14.6
<i>D. discolor</i>	.69	23.1	18.3	17.8	13.6	15.6	14.4	17.1
<i>Seiurus aurocapillus</i>	.75	20.2	17.6	13.8	11.2	13.7	13.6	15.0
<i>Geothlypis trichas</i>	.68	23.7	19.4	18.8	14.5	17.2	18.4	18.7
<i>Icteria virens</i>		15.7	14.3	14.7	10.6	12.9	13.4	13.6
<i>Passer domesticus</i>	.77	21.4	17.1	11.3	10.6	12.8	12.4	14.3
<i>Agelaius phoeniceus</i>	.71	16.3	13.8	9.9	8.0	10.6	9.9	11.4
<i>Icterus galbula</i>		22.2	17.4	14.7	10.7	13.7	13.7	15.4
<i>Quiscalus quiscula</i>	.75	15.7	13.0	10.2	7.8	10.5	10.4	11.3
<i>Molothrus ater</i>	.81	19.6	16.0	11.6	8.7	11.9	11.5	13.2
<i>Piranga olivacea</i>	.79	21.5	18.5	13.8	11.0	14.1	12.0	14.5
<i>Richmondia cardinalis</i>		20.3	16.7	13.7	10.6	13.7	12.0	14.5
<i>Pheucticus ludovicianus</i>	.76	20.5	17.0	13.4	9.0	12.3	12.5	14.1
<i>Pipilo erythrophthalmus</i>		18.8	15.7	10.7	9.9	12.8	14.2	13.7

TABLE III.—(continued)

Species	Avg. wt.	Fe.	Tt.	Avg. bone size				Ul.	Avg.
				Sc.	Co.	Hu.			
<i>Spizella passerina</i>	.73	22.9	18.6	14.7	11.4	14.0		13.6	15.0
<i>S. pusilla</i>	.74	22.5	19.4	13.7	11.7	13.8		14.2	15.0
<i>Melospiza georgiana</i>		20.4	17.0	13.4	13.1	13.6		14.9	15.4
<i>M. melodia</i>		18.1	15.7	13.6	10.2	12.9		13.1	13.9

¹ Expressed as ratio of hatchling weight/average egg volume.

² Expressed as per cent of adult bone length (Fe. = Femur; Tt. = Tibio-tarsus; Sc. = Scapula; Co. = Coracoid; Hu. = Humerus; Ul. = Ulnar; data derived from Table II).

used in ornithology to denote condition of development at hatching, are inapt in this kind of analysis. The altricial Philadelphia vireo and the precocial wood duck have the same neonatal bone size expressed as per cent of adult size. If the cartilages of the skeletal elements were included in these determinations, the altricial bird would have a great deal less distance to go than the precocial one in reaching adult size. It is patent, therefore, that in drawing comparisons between species of widely separated taxa the extent of development at hatching expressed in terms of per cent of adult development is underlaid by some radical evolutionary phenomena.

The neonatal bones examined in most of the song birds average 13 to 15 per cent of their adult lengths. Exceptions to that figure are as follows (Table III):

The low (8.7%) value for the common crow is probably not simply a function of the large size of this species, for the blue jay, of the same family, also has a moderately low value (12.0%). An examination of the neonates and consideration of the length of incubation indicates that the low value is also a function of relatively slow rate of prenatal development. Among the other species having low values in this respect are the dipper, red-winged blackbird, and common grackle (11.0%). The latter two have strong sexual dimorphism in size, *i.e.*, the male has an extended ontogenetic distance, which may account for a smaller size that is purely relative. The red-winged blackbird's delayed sexual maturity may be relevant in a consideration of slower developmental rate (proportionate to incubation period) of its embryos.

Three vireos have high values in Table III (21.4, 19.0, and 18.5%). As their neonatal bodies show heavy ossification, the values are probably a function of accelerated prenatal growth (but of moderately long incubation period). The answer to the puzzling question of why three of these vireos have natal down and three of them do not is apparently not tied to extent of bodily development (as expressed), for while the naked *Vireo griseus* and *V. bellii* have low values in Table III, the also naked *V. atricapilla* has a high value.

Another species having a high value is the yellowthroat (18.7%).

This species has a large egg for the size of the adult, a small neonate for the size of the egg, a short incubation period for its order, as well as a heavy ossification at hatching. The yellowthroat seems to be to the passerines what *Coturnix* is to the nonpasserines in respect to accelerated ontogeny.

There is no simple and direct correlation between adult body size of species and the neonatal bone size expressed as per cent of adult size.

RELATION OF EXTENT OF DEVELOPMENT AT HATCHING TO EXTENT AT MATURITY

Table IV presents two indices, which, when compared for each species, yield some measure of the degree of neonatal development for a certain character (ratio of humerus length to femur length). Column A shows that the humerus of the green heron has achieved at hatching only 52 per cent as much development as that of the femur. Column B shows that the adult humerus of the green heron is 138 per cent as large as the adult femur. Using this character throughout, a certain scale of relative precocity can be tentatively set up.

The American bittern is relatively further advanced than the green heron or the black-crowned night heron. The latter is less advanced than the green heron. One might postulate that ground nesting for the bittern may be conducive to greater precocity of the neonate.

Among the four Falconiformes examined, the black vulture is by far the more altricial. The other hawks show that the relative adult humeral lengths are proportionately reflected in the neonates. As hawks and herons are often called semi-altricial, it is of interest to note in Table IV that the herons are more precocial than the hawks.

In the Galliformes the domestic chicken is more precocious (for the character of shape under discussion) than is its ancestor, the red jungle fowl. The common coturnix, however, which by all other standards would seem to be highly precocious, is actually the least precocious of the lot.

An intriguing situation that should not be overlooked is that, where in evolution the adult may have come secondarily to resemble its specialized young (Wetherbee, 1958), precocity is determined more by evolutionary regression (of the adult) than by evolutionary progression (of the young). For example, no one can deny that the killdeer is extremely organized at hatching, but its organization when looked upon in terms of its adult characters is discordant; *i.e.*, the cursorial young killdeer is highly specialized for running. Its change in form during postnatal development is literally an ecologically based metamorphosis.

The gull and especially the tern are extremely altricial by the standards of Table IV; but this is more apparent than real, for actually the adults are highly specialized.

TABLE IV.—Reflection of adult characters (hu/fe) in extent of their development at hatching

Species	A ¹	B ²
<i>Butorides virescens</i>	.52	1.38
<i>Nycticorax nycticorax</i>	.53	1.54
<i>Botaurus lentiginosus</i>	.59	1.37
<i>Aix sponsa</i>	.41	1.68
<i>Coragyps atratus</i>	.46	1.54
<i>Buteo lineatus</i>	.69	1.46
<i>B. platypterus</i>	.62	1.41
<i>Falco sparverius</i>	.57	1.24
<i>Bonasa umbellus</i>	.72	.88
<i>Tympanachus cupido</i>	.60	1.02
<i>Colinus virginianus</i>	.59	.85
<i>Lophortyx californicus</i>	.66	.82
<i>L. gambelii</i>	.63	.82
<i>Coturnix coturnix</i>	.61	.92
<i>Phasianus colchicus</i>	.73	.91
Red Jungle Fowl	.63	.95
Domestic chicken (Columbian)	.89	.89
<i>Rallus limicola</i>	.61	.98
<i>Charadrius vociferus</i>	.40	1.48
<i>Philohela minor</i>	.57	1.16
<i>Larus argentatus</i>	.43	2.11
<i>Sterna hirundo</i>	.36	2.33
<i>Columba livia</i>	.55	1.11
<i>Zenaidura macroura</i>	.57	1.13
<i>Melopsittacus undulatus</i>	.58	1.03
<i>Bubo virginianus</i>	.62	1.56
<i>Chordeiles minor</i>	.42	1.68
<i>Archilochus colubris</i>	.44	.51
<i>Megasceryle alcyon</i>	.39	1.78
<i>Colaptes auratus</i>	.44	1.31
<i>Dendrocopus pubescens</i>	.43	1.35
<i>Tyrannus tyrannus</i>	.53	1.32
<i>Sayornis phoebe</i>	.58	1.28
<i>Empidonax minimus</i>	.58	1.15
<i>Eremophila alpestris</i>	.57	1.24
<i>Iridoprocne bicolor</i>	.53	1.11
<i>Riparia riparia</i>	.50	1.04
<i>Stelgidopteryx ruficollis</i>	.48	1.22
<i>Hirundo rustica</i>	.48	1.18
<i>Petrochelidon pyrrhonota</i>	.45	1.14

TABLE IV.—(continued)

Species	A ¹	B ²
<i>Cyanocitta cristata</i>	.65	1.02
<i>Corvus brachyrhynchos</i>	.55	1.30
<i>Parus atricapillus</i>	.65	1.10
<i>P. carolinensis</i>	.62	1.11
<i>Sitta carolinensis</i>	.66	1.20
<i>Cinclus mexicanus</i>	.68	1.07
<i>Troglodytes aedon</i>	.70	.94
<i>Thryomanes bewickii</i>	.74	1.03
<i>Thryothorus ludovicianus</i>	.69	.96
<i>Mimus polyglottos</i>	.61	1.06
<i>Dumetella carolinensis</i>	.70	.99
<i>Toxostoma rufum</i>	.63	.98
<i>Turdus migratorius</i>	.58	1.05
<i>Hylocichla mustelina</i>	.64	1.01
<i>H. fuscescens</i>	.67	1.01
<i>Sialia sialis</i>	.49	1.16
<i>Poliophtila caerulea</i>	.62	1.11
<i>Bombycilla cedrorum</i>	.57	1.08
<i>Lanius ludovicianus</i>	.63	1.05
<i>Sturnus vulgaris</i>	.53	1.10
<i>Vireo atricapilla</i>	.84	.98
<i>V. griseus</i>	.74	1.06
<i>V. bellii</i>	.70	1.01
<i>V. olivaceus</i>	.59	1.10
<i>V. philadelphicus</i>	.65	1.06
<i>V. gilvus</i>	.57	1.11
<i>Mniotilta varia</i>	.61	1.09
<i>Dendroica petechia</i>	.69	.98
<i>D. discolor</i>	.68	1.06
<i>Seiurus aurocapillus</i>	.68	1.08
<i>Geothlypis trichas</i>	.73	.93
<i>Icteria virens</i>	.82	.95
<i>Passer domesticus</i>	.59	1.03
<i>Agelaius phoeniceus</i>	.64	1.11
<i>Icterus galbula</i>	.62	1.05
<i>Quiscalus quiscula</i>	.67	1.04
<i>Molothrus ater</i>	.61	1.12
<i>Piranga olivacea</i>	.66	1.13
<i>Richmondia cardinalis</i>	.67	1.04
<i>Pheucticus ludovicianus</i>	.60	1.07
<i>Pipilo erythrophthalmus</i>	.68	.97

TABLE IV.—(continued)

Species	A ¹	B ²
<i>Spizella passerina</i>	.61	1.16
<i>S. pusilla</i>	.61	1.05
<i>Melospiza georgiana</i>	.67	.91
<i>M. melodia</i>	.71	.98

¹ Extent of potential development humerus has achieved at hatching (neo. hu./ad. hu.) expressed as ratio of extent of potential development femur has achieved at hatching (neo. fe/ad. fe), *i.e.*, ratio of per cents.

² Length of adult humerus expressed as ratio of length of adult femur, *i.e.*, ratio of sizes.

Among the swallows the bank and the tree swallow seem to be the more altricial in Table IV, although the fact of the matter is that the young of all swallows are practically identical. At this point in the analysis one is forced by weight of the accumulated evidence to resume the use of quotation marks around "altricial" and "precocial," for it is evident that the whole life history of the organism and its biogenetic burden are involved in any real understanding of the developmental condition of young at hatching. For further discussion see Wetherbee (1958).

CONCLUSIONS

The following general conclusions are drawn from the data:

1. Mouth markings in neonates, common in Old World species, were found in only four New World species: catbird, horned lark, blue-gray gnatcatcher, and black-billed cuckoo. Mouth color of neonates is perhaps partly the result of blood capillary beds, at least in the field sparrow. As parabronchi are poorly developed in "altricial" neonates, the mouth lining may serve as an accessory respiratory organ. Neonates of most bird species weigh 72 to 78 per cent of the weight of the egg (at specific gravity of unity) from which they hatch. As neonatal brown-headed cowbirds are heavy in proportion to the eggs from which they hatch, social parasitism may put selective pressure on length of incubation period and/or the amount of neonatal yolk. The neonatal blue jay, heavy in proportion to the egg from which it hatches, seems to have a slowing of body development relative to incubation period. The proportionately light neonate of the wood thrush on the other hand may be caused by an extended incubation period. The wood warblers, especially the yellowthroat, have unusual growth patterns comparable with that of the common coturnix: large egg for the size of the adult, small neonate for the size of the egg, short incubation period for its taxon, and advanced development at time of hatching.

2. Volume of egg does not affect the extent of development at

hatching within a species nor affect the length of incubation period at least appreciably within a species.

3. Most passerine birds have incubation periods between 280 and 370 hours. Examples of extremes are: blue jay, 406 hours, and yellowthroat, 256 hours. These incubation periods show very little variation under standardized conditions and are species specific.

4. The longer passerine incubation periods produce the more helpless neonates, and the shorter periods produce the most advanced neonates. Therefore, although a fast rate of embryonic development may shorten the incubation period, a long incubation period does not produce a further advanced neonate.

5. Commencement of incubation by the parent before the last egg of the clutch is laid probably exerts selective pressure for short incubation period because of intrabrood competition. The altricial condition in birds may have arisen through this mechanism. In conjunction with the genetic mechanisms of poicilogony (foetalization of adults) the selective mechanism above may provide a rather full understanding of the evolution of infants.

6. The qualities generally described by the terms "precocious" and "altricial" are less apt for species than for individual characters. Contrary to general understanding, some "altricial" birds have less ontogenetic distance to traverse in reaching maturity than some "precocious" birds.

7. Neonatal bone lengths (of the six bones examined) range from 4 per cent (coracoid, yellow-shafted flicker) to 48 per cent (tibiotarsus, killdeer) of their adult lengths. The killdeer is the species with the highest average bone length (30% of adult size) at hatching ("the most precocious bird"). The crow is the "most altricial" (8.7% of adult size). Passerine species having the smallest neonatal bone sizes (expressed as per cent of adult sizes) in addition to the crow are dipper, red-winged blackbird, and common grackle (11%). The black-capped, red-eyed and Philadelphia vireos, and the yellowthroat are the passerine species having the largest neonatal bone sizes, 18.5 to 21.4 per cent.

8. The extent of development at hatching is determined not only by the rates of character developments in the embryo and by the length of incubation period but also by the magnitude of total ontogenetic distance that adulthood represents for each character of each species; i.e., the whole life history of the organism and its biogenetic burden are involved in any real understanding of the developmental condition of young at hatching.

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The Genus *Skrjabinopsolus* (Trematoda: Digenea), with Reference to the Allocreadioid Problem¹

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ABSTRACT: In young adults of *Skrjabinopsolus manteri*, the excretory system has three flame cell groups per quadrant and other features like that of *Deropristis inflata*. The miracidium of *S. manteri* has one pair of flame cells and lacks an eyespot. Extensive morphological and ecological studies strongly suggest that the cercaria is the species previously reported for *Allocreadium ictaluri*; it encysts with little development in freshwater oligochaetes, on which the sturgeon feeds. In its embryology, the primary excretory pores develop in the tail of the cercaria a short distance from the body, thereby supporting the allocation of *Skrjabinopsolus* and related genera to a distinct family, the Deropristiidae. That family is redefined to include *Deropristis*, *Pristicola*, and *Skrjabinopsolus* in the Deropristiinae and *Cestrahelminis* as type and only genus in a new subfamily, Cestrahelmininae.

INTRODUCTION

The diversity of life histories and larval stages of trematodes that La Rue (1957) has assigned to the superfamily Allocreadioidea poses a major problem in the taxonomy of the Digenea. A group that is pertinent to that problem contains species of *Skrjabinopsolus* and related genera whose taxonomic position has been in dispute. One life history is known, that of *Deropristis inflata* reported by Cable and Hunninen (1942). The writer's observations indicate the probable life history of another species, *Skrjabinopsolus manteri*, which Cable (1952) described as a common parasite of the Shovelnose Sturgeon in the Wabash River. Its cercaria is believed to be the one described by Seitner (1951) as the larva of *Allocreadium ictaluri* but shown not to be such by the writer (Peters, 1957). As nothing is known concerning the embryology of the excretory system in the group, that aspect was investigated along with the life cycle of *S. manteri* for information bearing on the status of its group in the allocreadioid complex.

The genus *Skrjabinopsolus* was erected by Ivanov and Murygin (1937) to include *S. acipenseris* from sturgeons of the Volga River delta as type species and supposedly *Distomum semiarmatum* Molin, 1858, as a second species. Another, *S. skrjabini*, was reported from sturgeons of the Black Sea by Osmanov (1940) and differentiated from *S. acipenseris* in having a prepharynx and a greater posterior extent of the uterus. However, Bykhovskii and Dubinina (1954) examined specimens from sturgeons in both the North Caspian and Black seas and reduced *S. skrjabini* to synonymy with *S. acipenseris*.

¹ Based on part of a thesis submitted for the Ph.D. degree, Purdue University, August, 1960, and prepared under the direction of Professor R. M. Cable.

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Although their conclusion appears valid to the writer, Skriabin (1954) regarded the problem of speciation in the genus *Skrjabinopsolus* as still unsolved. It may be that *S. semiarmatum*, if better known, would prove to be the only valid European species of its genus. Molin (1858) reported it briefly from *Acipenser naccari* and extended his observations somewhat in a later report (1861). There is no known feature of the species which would exclude it from *Skrjabinopsolus*, and the heavy cuticular armature, sessile ventral sucker, and especially the spiny cirrus suggest its inclusion in that genus. Osmanov (translated from Markevich, 1951) supports that view, as follows:

"It is exceedingly possible that *Skrjabinopsolus skrabini* n. sp. is identical with *Distomum semiarmatum* Molin, 1858, from *Acipenser sturio*. Consequently we regard our species as provisional for the present."

The only other species recorded for the genus is *S. manteri* which is very similar to *S. acipenseris* but differs from that species in having a much longer body with the ovary more anterior and eggs that average slightly smaller in size.

The occurrence of such similar trematodes only in sturgeons, and from such widely separated localities, is a striking example of host specificity among the digenetic trematodes and parallel evolution of host and parasite. Because a common gene pool cannot be shared by parasites of the strictly freshwater sturgeon in the Wabash River and those of Eurasian sturgeons, it is concluded that, although very similar, *S. acipenseris* and *S. manteri* are distinct species.

EVIDENCE CONCERNING THE LIFE CYCLE OF *SKRJABINOPSOLUS MANTERI*

The difficulties posed by Seitner's (1951) account for the life history of *Allocreadium ictaluri* were discussed by Cable (1956), who pointed out that the cercaria described by Seitner is much like that of *Deropristis inflata*, as indeed Seitner had observed. Because closely related trematodes often have extremely similar life cycles and the cercaria of *D. inflata* encysts in a marine annelid, fresh-water oligochaetes were collected from the Wabash River and examined for a metacercaria similar to that of *D. inflata*; such was quickly found and thereafter proved to result from the penetration and encystment of the cercaria described by Seitner. As in *D. inflata*, the metacercaria does not increase in size or develop appreciably except in spination, which becomes more conspicuous. The large excretory concretions remain intact.

The writer has confirmed Seitner's observations that the cercaria will penetrate clams but found that the resulting metacercariae were dead after four days. It is evident that oligochaetes serve as the natural second intermediate host of the species, and those annelids are eaten in large numbers by the sturgeon. Furthermore, an extensive

examination of oligochaetes from mud bottom areas of the Wabash River has revealed but the one species of metacercaria.

The adult of the metacercaria in question could not be determined experimentally because sturgeons known to be free of *S. manteri* were not available and metacercariae fed to other fishes failed to infect them. As practically all Shovelnose sturgeons examined from the Wabash River were infected, attempts were made to remove the worms by treatment with gentian violet and piperazine, but without success. When infected annelids were force-fed to sturgeons, large numbers of very young worms were recovered from the spiral valve, along with larger ones from previous natural infections, but there were all gradations in size and development. Furthermore, similar gradations occurred in the many worms from a natural infection in one fish that had been held in captivity for 34 days. Thus, the parasites grow very slowly in captive sturgeons, and inability to keep them alive for extended periods made it impossible to utilize the method of superimposing an experimental infection on a natural one and later distinguishing between the two.

Negative results were obtained when metacercariae were fed to other fishes, including the gar, the rock bass, the mud minnow, and a few ictalurid species. Inability to infect catfishes is further evidence that the cercaria in question is not the larva of *Allocreadium ictaluri*. Moreover, failure of other fishes to become infected agrees with the evidently high degree of host specificity of *S. manteri* as indicated by the examination of a large variety of fishes and other animals from the locality over a number of years and finding that trematode only in the sturgeon.

Attempts to demonstrate the life cycle by infecting the mollusk host also were unsuccessful. First of all, it could not be established whether the egg normally hatches in the open or must be eaten by the mollusk. On one occasion, eggs in intestinal mucus stained green with bile pigments were placed in a dish submerged in slowly moving water. The following day nearly all eggshells were empty with the operculum loosened, but no miracidia could be found. From that observation, it was believed that the eggs normally hatch in the open but the experiment was repeated many times without further evidence to that effect. Unsuccessful also were attempts to induce hatching by shaking, both rapid and slow temperature changes, and the osmotic effects of transfer back and forth from water to 0.7 per cent saline. Although no hatching occurred, the larvae survived such treatments. Following the suggestion of Tromba (1954), eggs were placed in 0.85, 3.0, and 10.0 per cent formalin, but no hatching occurred within ten minutes. With Sørensen's phosphate buffer solutions varying from pH 5.3 to 8.0, a few eggs hatched only at pH 6.5 but the miracidia died quickly, partly extruded from the eggshell or lying close to it. Finally, hatching was not induced by mixing eggs with the body fluids of *Pleurocera acuta*, *Campeloma rufum*, or *Goniobasis livescens* or by leaving them in water with much organic debris, a

method that the writer found effective in inducing eggs of *Allocreadium* species to hatch.

Embryonated eggs fed to *Pleurocera acuta* of various sizes, *Goniobasis livescens*, *Campeloma rufum*, and *Amnicola limosa* were passed with the snails' feces, often in large numbers, but were almost invariably unhatched. Those snails that passed open eggshells were maintained for a few days to two months in the laboratory and were then cracked and examined but no stages were found that could be attributed to experimental infection.

Although attempts to complete the life history of *S. manteri* experimentally were inconclusive, circumstantial evidence indicates that the cercaria and metacercaria under consideration are larval stages of that species. In the first place, there is complete morphological agreement in respect to the digestive and excretory systems, eyespot pigment, and body spination. Furthermore, the characteristic excretory concretions of the cercaria are retained through the metacercarial stage and were seen in young adults from naturally infected sturgeons. A biocellate cercaria is established by the remnants of eyespots in the adult and that fact rules out of consideration as the larval stage most of the freshwater cercariae. The remaining ones, i.e., those with eyespots, are of but a few types in fresh water (monostomes, amphistomes, opisthorchioid larvae, ophthalmocephalid cercariae, and a few furcocercous and gymnocephalous species), for nearly all of which the general life history and the systematic group to which the adult belongs are rather well understood. On that basis, all of the biocellate cercariae known to develop in Wabash River mollusks except the one described by Seitner (1951) can be excluded as the larva of *Skrjabinopsolus manteri*. Further circumstantial evidence is the correlation between the presence and abundance of the various stages in certain localities. Where the cercaria, metacercaria, and adult were sought, all were either present or absent in a given locality and if present, their relative abundance is roughly what one would expect of stages belonging to the same life cycle.

STAGES IN THE LIFE CYCLE OF *SKRJABINOPSOLUS MANTERI* (Measurements in millimeters)

ADULT

The description of *S. manteri*, as given by Cable (1952), is supplemented by the writer's observations on the excretory system. In young adults (Fig. 14), it is very similar to that system in *D. inflata*, as described by Cable and Hunninen (1942). The excretory pore leads into a short, saccate bladder confined to the post-testicular region. The posterior ends of the primary excretory ducts are ciliated and enter the bladder anterolaterally to continue along its internal surface and open near the mid-level. Anteriorly, the ducts extend with convolutions to the level of the cirrus sac, where each receives an an-

terior and a posterior secondary tubule; capillaries from three groups of flame cells join each secondary tubule and, as in *D. inflata*, are not dichotomous in arrangement within the flame cell groups. One flame cell of the posterior-most group is considerably larger than others of that group. The maximum number of flame cells seen in young adults is given in the formula $2 [(3+7+14) + (11+12+8)]$ but increases with growth of the worm. In very old worms, the excretory tubules and capillaries are delineated by a pigment which is distinct in both living specimens and whole mounts.

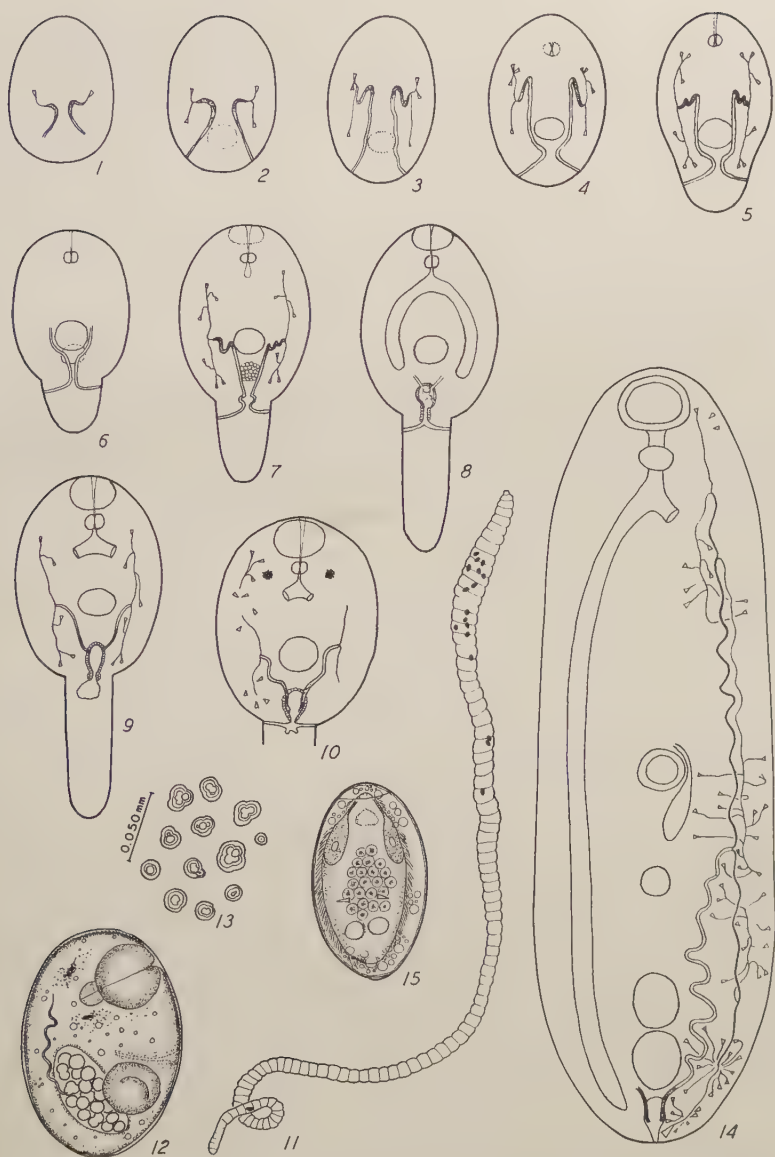
EGG AND MIRACIDIUM

The eggs freshly laid by adults placed in 0.7 per cent saline measure 0.043-0.051 by 0.023-0.026; the shell is yellow, operculate, and has a small antopercular knob (Fig. 15). Certain details of the miracidium were observed through the eggshell. A cephalic gland with a distinct nucleus occurs on each side; it is variable in length but always pre-equatorial. An eyespot is lacking. The two flame cells lie near the midlevel, among a group of over a dozen germinal cells. Commonly observed were two larger vacuole-like structures, possibly excretory reservoirs. Cilia cover the entire surface but are inactive unless pressure is applied to the egg.

CERCARIA

The description of the cercaria given by Seitner (1951) is supplemented here to include the embryology of the excretory system because of its significance in La Rue's (1957) scheme of classification.

Development of the excretory system begins in the germinal ball with the appearance of a pair of flame cells, each with a duct containing a patch of cilia but apparently not opening to the surface (Fig. 1). By the time that the primordium of the ventral sucker appears in the posterior half of the embryo (Fig. 2), there are two pairs of flame cells which beat more slowly than the ciliary patches, and the collecting ducts open posterolaterally. Somewhat later (Fig. 3), there are two relatively large anterior flame cells and a smaller posterior one on each side and the ciliary patch is limited to the recurrent anterior end of the primary collecting duct. As the anterior flame cells increase to three per side (Fig. 4), the primary ducts converge posterior to the ventral sucker and the outline of the pharynx is seen. With elongation of the embryo (Fig. 5), the number of posterior flame cells increases to three on each side. The primordium of the bladder epithelium (Fig. 6) appears posterodorsal to the ventral sucker by the time the tail bud is evident. The excretory ducts posterior to the sucker come very close together to extend into the tail bud and then diverge to open laterally a short distance from the body-tail furrow. With elongation of the tail and appearance of the primordium of the oral sucker (Fig. 7), the excretory ducts form a small lateral convolution near the furrow and



Figs. 1-15. —1-10. Embryology of the excretory system of the cercaria that probably is the larva of *Skrjabinopsolus manteri*. 11. Location of metacercariae in an experimentally infected oligochaete. 12. Ten-day-old metacercaria. 13. Excretory concretions from bladder of 16-day-old metacercaria. 14. Excretory system of young adult *S. manteri* from a natural infection. 15. Egg and miracidium of *S. manteri*.

then fuse to form the bladder (Fig. 8) at about the time that the intestinal ceca appear. Without the flame cell number increasing, the bladder then becomes distinctly epithelial with the ciliary patches of the ducts immediately anterior to it (Fig. 9). An atrium forms in the anterior part of the tail and the primary excretory pores disappear. When eyespot pigment is apparent (Fig. 10), the ciliated ends of the ducts extend into the bladder, the number of flame cells increases, and a secondary excretory pore forms at each side of the body-tail furrow. With further development, the flame cells increase to the number observed in emerging larvae and concretions appear in the bladder. The cuticular spines do not develop until shortly before emergence.

METACERCARIA

Naturally infected annelids were found in the Wabash River at Lafayette and Covington, Indiana. Metacercariae in them were never further developed than those of eighteen-day experimental infections and were mostly in the region of the genital organs (Fig. 11). In one case, a reddish-brown secondary cyst wall was seen, but in general there is very little host tissue response. Several species of oligochaetes, mainly tubificids, serve as natural hosts. Each worm usually contained 1-4 cysts, but 17 were seen in one from Covington.

When oligochaetes are exposed to infection, cercariae may begin to penetrate them almost immediately or may crawl about on the surface for a time but not evidently seeking a particular site to enter. Five to ten minutes are required for penetration; decalcification occurs at the end of the process. Thereafter, the metacercaria migrates at random for two hours or longer, stopping occasionally as if about to encyst but then moving further to do so.

The cyst (Fig. 12) is oval, measures 0.160-0.260 by 0.087-0.110, and does not change appreciably in size with age although its primary wall increases from about 0.001 to 0.004 in thickness by the eighteenth day. The comparatively little development of the metacercaria within the annelid is confined largely to a slight increase in the size of the suckers and pharynx, less vacuolation of the parenchyma, dispersal of the eyespot pigment, and growth of the cuticular spines to a length of up to 0.005 as the entire body becomes spinose. The excretory concretions of the cercaria (Fig. 13) are retained with little change except in size and are composed of concentric layers of a substance that dissolves in weak hydrochloric acid.

DISCUSSION

Species of the genera *Skryabinopsolus*, *Deropristis*, and *Pristicola* undoubtedly form a natural group, the Subfamily Deropristiinae Cable and Hunninen, 1942, whose family status has been in dispute. Most recent authors have assigned those genera to the Family Acanthocolpidae (Skryabin, 1954; Bykhovskii and Dubinina, 1954; Dawes,

1956; Yamaguti, 1958), although *Deropristis* had been excluded from that family by Cable and Hunninen (1942), a view accepted by Caballero (1952) and reiterated by Cable (1952, 1955). Adults of the Deropristiinae, however, differ from genera of the Lepocreadiinae and Homalometrinae in the extent of the uterus and vitellaria and in spination of the cirrus and metraterm. On the basis of differences in adult morphology, Skriabin (1958) reversed his earlier view (1954) and removed the genera *Deropristis*, *Pristicola*, and *Skrjabinopsolus* from the Acanthocolpidae, erecting for them the Family Deropristidae. That conclusion has been reinforced by the writer's studies on the embryology of the excretory system of acanthocolpid and lepecreadiid cercariae (Peters, in press) as well as of the species just considered and believed to be the larva of *S. manteri*. All three differ with respect to the location of the primary excretory pores.

Skriabin (1958) did not include in the Deropristidae the genus *Cestrahelmins* Fischthal, 1957, which has more in common with that family than with any other group but differs from the other three genera to the extent that it is considered to represent a distinct subfamily. For that reason the family is redefined and divided into subfamilies as follows:

Family Deropristiidae Skriabin, 1958, emend.

Diagnosis.—Distomes with spinose cuticle, spines sometimes locally enlarged to form patches or a ventrally interrupted collar near anterior end but not adjacent to mouth. Cercarial eyespot pigment present. Mouth subterminal, pharynx and esophagus present, ceca extend at least to level of testes and usually beyond. Excretory vesicle saccate, with posterior pore; flame cells, where known, in three anterior and three posterior groups on each side. Genital pore at edge of ventral sucker, median or displaced to left. Cirrus sac with spiny cirrus, pars prostatica, and saccate seminal vesicle that is usually bipartite. Testes two, well within hindbody. Ovary pretesticular; independent seminal receptacle and Laurer's canal present; vitellaria not extensive, between level of pars prostatica and post-testicular space, usually not reaching posterior testes. Uterus extends posteriorly at least to level of anterior testis and may fill hindbody; metraterm distinct, with very small to prominent spines; eggs moderately numerous to numerous. Adults in intestine of marine and fresh-water fishes. Cercariae biocellate, stylet lacking in known ones; bladder epithelial but not with prominent gland-like cells, large concretions present; primary excretory pores, where known, just posterior to body-tail furrow. Cercariae develop in simple rediae in prosobranch gastropods. Includes the subfamilies:

Subfamily Deropristiinae Cable and Hunninen, 1942

Diagnosis.—With the characters of the family. Esophagus short, intestinal bifurcation well anterior to ventral sucker; ceca long, reach-

ing posterior end of body. Genital pore median; seminal vesicle distinctly bipartite; pars prostatica small, tubular.

Type Genus.—*Deropristis* Odhner, 1905; other genera: *Pristicola* Cable, 1952; *Skrjabinopsolus* Ivanov in Ivanov and Murygin, 1937 (Syn. *Pristotrema* Cable, 1952).

Cestrahelminae n. subfam.

Diagnosis.—With the characters of the family. Esophagus long, intestinal bifurcation near level of ventral sucker, ceca not reaching posterior end of body. Genital pore well to left of midline; seminal vesicle not distinctly bipartite; pars prostatica prominent, bulbous.

Type and Only Genus.—*Cestrahelmins* Fischthal, 1957.

The writer examined the type specimen and sectioned material of *Cestrahelmins laruei* and found that what Fischthal (1957) described as the "inner" thick-walled division of the seminal vesicle actually is the pars prostatica and that the seminal vesicle is not distinctly bipartite, as in other species of the Deropristiidae. Careful focusing on the whole mount revealed a slight constriction that indistinctly separates the anterior part with a slightly thickened wall from a thin-walled posterior portion. In the sectioned specimen, however, such a constriction was not evident, although the difference in the wall thickness of the vesicle was apparent, the posterior end being extremely thin and difficult to distinguish from the cirrus sac itself.

The writer concurs with Skriabin (1958) in withholding judgment as to allocation of *Paratormopsolus* Bykhovskii and Dubinina, 1954, until that genus is better known. The posterior extent of the uterus and relatively scanty vitellaria are in agreement with the Deropristiidae but the external seminal vesicle and unarmed cirrus and metraterm are characteristic of the Lepocreadiidae, the family to which the Deropristiidae is most closely related.

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The Lateral-Line System in the Rio Grande Perch, *Cichlasoma cyanoguttatum* (Baird and Girard)¹

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ABSTRACT: The lateral-line system of *Cichlasoma cyanoguttatum* is similar to that of other perciforms but there are many peculiarities. The tubes of the lateralis scales do not make contact with each other but the innervation of the organs in this part of the system is normal. The external morphology and osteological components of the system are described in detail and compared with that of serranids and centrachids; the text is copiously augmented with illustrations. The lozenge-shaped canal neuromasts are in general like those of sunfishes but much larger. The sensory cells, unlike most of the cells seen in other fishes, bear multiple sensory hairs. All of the supporting cells penetrate to the free surface of the organ and intercellular bridges connect each with the others, thus forming a kind of syncytium.

Cichlasoma cyanoguttatum is the only member of the family Cichlidae known to occur naturally in continental United States. Its range extends eastward from the Rio Grande in Texas as far north as the Rio Colorado near Austin. Material for this study was collected from the Blanco River, 25 miles northwest of San Marcos and from San Marcos Springs, Hayes County on July 14, 1958. Dr. Kirk Strawn of Lamar Institute of Technology, Beaumont, Texas, assisted in the collecting and Dr. G. A. Moore of Oklahoma State University offered helpful criticisms. I am grateful for their assistance.

Several specimens were fixed in PFA₃, one of Allen's modifications of Bouin's fluid, and others in 10 per cent formalin. Three of the formalin-fixed specimens were stained by the alizarin method of Hollister (1934). In addition, four large specimens were packed in dry ice and subsequently disarticulated for bone study. Other formalinized fish were dried by means of jets of air and the canal system injected with India ink. Innervation was determined by gross dissection under the lens of a stereomicroscope. The lachrymal bone was chosen for microscope sections because of its constancy and ease of removal. Material for sectioning was decalcified in two per cent hydrochloric acid, embedded in pyroxylin and cut at five microns. Some sections were stained with iron hematoxylin and others with Mallory's triple connective tissue stain; all were mounted in picrolyte. Measurements were taken by means of a filar micrometer mounted on a compound microscope. Drawings were made with the assistance of a camera lucida.

EXTERNAL MORPHOLOGY

In its external appearance the cephalic lateral-line system of *Cichlasoma* is similar to that of other perciform fishes (Stensiö, 1947;

¹ Contribution No. 301 from the Zoology Department and Research Foundation, Oklahoma State University. Supported by National Science Foundation Grant G-4323.

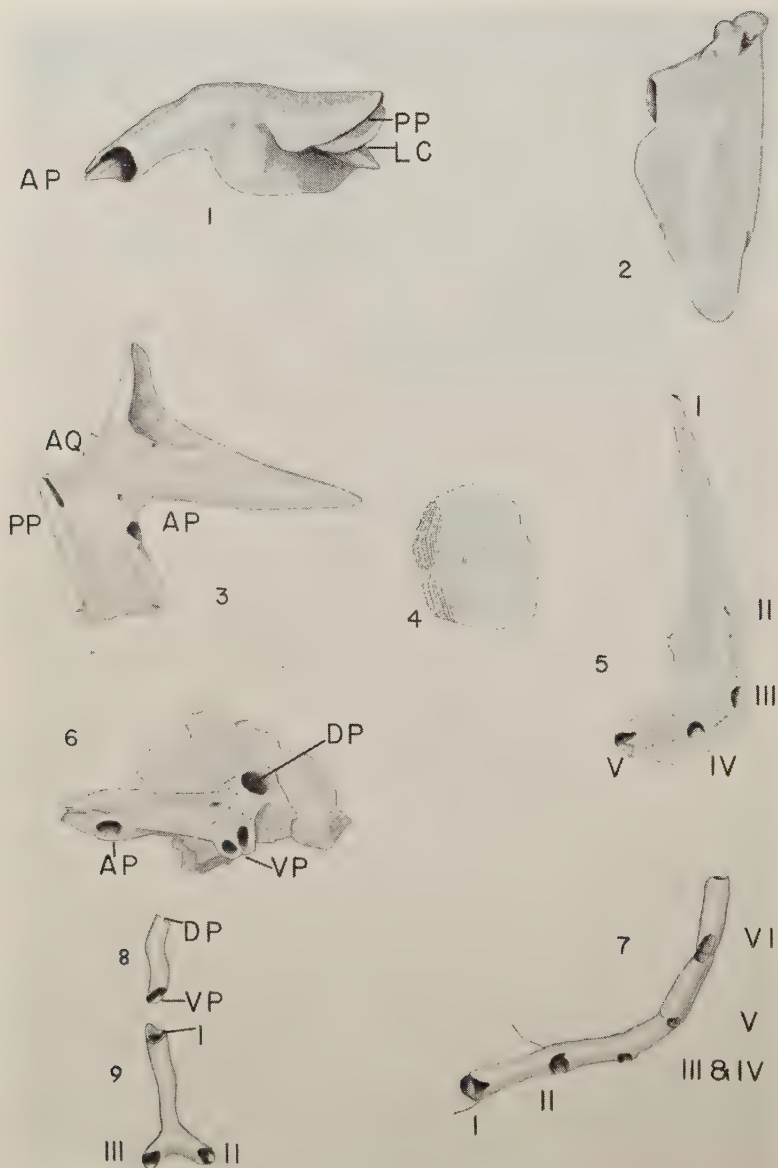
Holmgren, 1942; Moore, 1956). All of the usual components are present, except the supratemporal commissure of some fishes, which is here much abbreviated. The nomenclature employed is modified from Hubbs and Cannon (1935). Throughout the system, with the exception of the secondary branches from the main canals of the lachrymal, frontal, dentary and the preopercle, all of the external canaliculi (branches) arise where two bones meet. The sensory organs contained in the canals are never formed in the branches, but instead form midway between the two ends of a main canal in the case of a simple bone, or midway between two side branches in the case of a compound one.

The coronal pore (MP) of the supraorbital commissure (Fig. 14), in specimens injected with India ink, appears to be an isolated opening on the median line, slightly behind the middle of the eye. In other words, the connection between the pore and the rest of the system is not apparent as it is in sunfishes and serranids. The reason for this will be shown below in the discussion concerning the osseous elements of this system. This commissure is the only canicular connection from one side of the fish to the other.

In sunfishes, with a few exceptions, such as the mud sunfish, *Acantharchus pomotis*, the cephalic lateral-line canals are not covered by scales. On the other hand, in the Rio Grande perch, all of the canals except the supraorbital, infraorbital and the canaliculi (mainly in the skin) are overlaid by scales.

THE LATERALIS

At the junction of the cephalic lateral-line with the lateralis there is a ventrally-directed canaliculus (Fig. 12). This is reminiscent of a similar condition in *Pomoxis annularis*, but in general, sunfishes lack such openings. Posteriorly to this point the lateralis is composed of short tubes borne by modified scales (Fig. 4) as in other fishes. However, unlike the centrarchid lateralis, the tube in each scale makes no connection with those of other scales in the series. It is necessary to fill the tube in each scale separately in effecting India ink injections. Observation of cleaned and mounted scales, stained with carmine, reveals small canals open at each end (lacking the side branches that many sunfishes possess) and borne approximately upon the center of each lateralis scale. The neuromasts (Fig. 4) are located about midway between the ends of each tube. In addition to this disjunct arrangement, the lateralis abruptly ends at a position under the sixth or seventh dorsal fin ray from the posterior end of the fin. Two scale rows below this point another series of tubes begins and continues onto the caudal peduncle, where it ends, a few scales anterior to the caudal fin. The upper series overlaps the lower by two pored scales and, in all of the specimens observed, contained 19 tubes; the lower series, which is nearly in a straight line, contained ten tubes. It is supposed that this sort of arrangement is of general occurrence in cichlids since it was also observed in



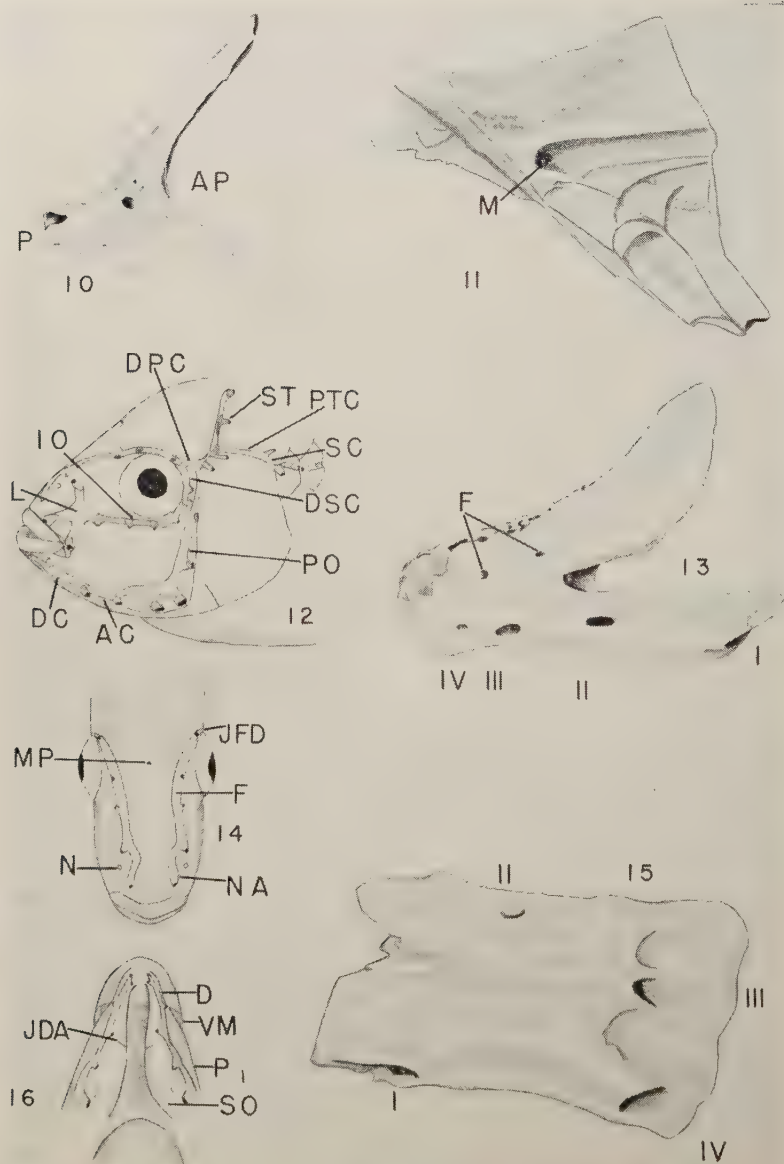
Figs. 1-9.—Lateral line system of *Cichlasoma cyanoguttatum*. 1. Nasal bone $\times 5$. AP, anterior lateral-line opening; LC, chamber under posterior opening; PP, posterior lateral-line opening. 2. Supracleithrum $\times 3.7$. Anterior on right. 3. Articular $\times 5$. AP, as in Fig. 1; AQ, articular surface for anterior facet of the quadrate; PP, as in Fig. 1. 4. Lateralis scale $\times 1$. Anterior on right. 5. Preopercle $\times 2.2$. I-V, lateral-line openings; I, dorsal; V, antero-ventral. 6.

Tilapia nilotica, in the oscar, *Astronotus ocellatus*, and the angelfish, *Pterophyllum eimekei*, all cichlids.

OSTEOLOGICAL COMPONENTS

For proper interpretation of any lateral-line system one must pay particular heed to the bones involved, all of which are of dermal origin. The terminology utilized for the lateral-line bones is that of Harrington (1955). From the trunk the lateral line enters the head region by penetrating the dorsal extremity of the supracleithrum (Fig. 2), which, in a lateral aspect, is roughly acutely triangular. The canal is more capacious posteriorly than anteriorly and is completely enclosed in bone. This arrangement is in general like that of serranids (Woolcott, 1957) and in the Sacramento perch (Dineen and Stokley, 1956) and several other sunfishes (unpublished). The anterior end of the bony canal is in fairly close approximation to the ventral opening of the posttemporal, through which the canal continues its course anteriorly. The posttemporal (Fig. 10) is likewise similar to the same bone in serranids and centrarchids except that its posterior end is smooth, whereas in serranids and in *Archoplites* it bears few to many serrae. Another dissimilarity is that the posterior end of the bone bears two pores in sunfishes and serranids; in *Cichlasoma* there is but a single pore. The anterior opening, surrounded by slight hillock of osseous material, delivers the canal to the supratemporal-intertemporal, a small, tubular, inverted Y-shaped bone which is pored at all three ends of the "Y" (Fig. 9). The anterior arm communicates with the dermopterotic and the dorsal extension with the tubular lateral-extrascapular (Fig. 8) which is slightly sigmoid in shape. In sunfishes these two bones are often in the form of open channels. The dermopterotic (Fig. 6) is represented as a blade-like, lateral extension from the pterotic. It is roughly a horizontal-Y in shape and bears three or four lateral-line openings, according to whether the ventral pore is double or single. The dorsal opening communicates with the lower one of the supratemporal-intertemporal; the ventral one or two with the superior end of the preopercle; and the anterior end opens into a common sinus contained in the connective tissue at the postero-dorsal aspect of the eye, where the dermosphenotic and frontal components also communicate (Fig. 12). This bone is similar to that of centrarchids, but it is always completely tubular, whereas in sunfishes it is often seen as an open groove. Furthermore, in sunfishes there are rarely more than two openings, a posterior and an anterior one, the

Dermopterotic and pterotic $\times 5.3$. VP, ventral lateral-line opening; AP, PP, as in Fig. 1. Anterior on left. 7. Infraorbital ossicles $\times 6.7$. II, Jugal III & IV, compound ossicle; V, ossicle 5; VI, Dermosphenotic. 8. Lateral extrascapular $\times 6$. DP, dorsal lateral-line opening; VP, as in Fig. 6. Anterior on left. 9. Supratemporal-intertemporal $\times 6$. I, dorsal lateral-line opening; II, posterior lateral-line opening; III, anterior lateral-line opening.



Figs. 10-16.—Lateral line system of *Cichlasoma cyanoguttatum*. 10. Post-temporal bone $\times 5$. AP, P, as in Fig. 1. 11. Median view, left frontal bone $\times 4.7$. M, median lateral-line opening. 12. Left, antero-lateral view of head $\times 1.7$. AC, articular component of operculo-mandibular canal; DC, dentary component of operculo-mandibular canal; DPC, dermo-pterotic component of the cephalic

communication with the upper end of the preopercle being accomplished from the simple opening in the side of the canal.

From its junction with the dermopterotic to its anterior extremity, the lateral-line passageway borne by the preopercle (Fig. 5) is completely enclosed in bone, except for very short continuations where lateral branches are given off. This canal appears as a slight elevation on about the center of the plate-like body of the preopercle, the upper end being tubular in nature. There are five openings, two terminal and three side-branches. The two anterior-most side branches are surrounded by bone for most of their length and a spongy-appearing osseous material fills in between them. At its anterior end the preopercle is moderately deflected ventrad where it couples with the posterior end of the articular.

In general shape the preopercle (Fig. 5) is not unlike that of serranids and centrarchids, this being about as far as the homology can be carried. The centrarchid preopercular lateral-line canal seldom has the side branches surrounded by bone, these being continued from a slit-like opening to the edge of the bone by connective tissue canaliculi. Furthermore, instead of this particular canal being a solid tube, as it is in *Cichlasoma*, it appears as a simple fold, i.e., as if one had folded a flat piece of bone upon itself, the free edge of the fold being directed caudad. In both Serranidae and Centrarchidae the posterior edge of the preopercle bears conspicuous serrae; these are lacking in *Cichlasoma*.

Slightly in advance of the anterior end of the preopercle the canal enters the articular (Fig. 3), which is shaped about like its homologue in the Centrarchidae. The canal passes downward at a declivitous angle to the point where it leaves the bone to enter the dentary (Fig. 13). The last-named bone is similar to the same bone in sunfishes, being approximately intermediate between a species with a short rostrum, such as *Lepomis macrochirus* or *L. megalotis*, and one with a long rostrum, as *L. cyanellus* or *Chaenobryttus gulosus*. The most obvious difference between centrarchid species and *Cichlasoma* in this respect is the number of lateral-line openings in the bone. The dentary of the Rio Grande perch possesses only four of these openings whereas most centrarchids have five. This is very obvious, even

lateralis canal; DSC, dermo-sphenotic component of the infraorbital canal; 10, infraorbital canal; L, lachrymal component of the infraorbital canal; PO, preopercular component of the operculo-mandibular canal; PTC, posttemporal component of the cephalic lateralis; SC, supracleithral component of the cephalic lateralis; ST, supratemporal (lateral extrascapular and supratemporal-intertemporal) components of cephalic lateralis. 13. Dentary bone $\times 5.2$. F, foramina; I-IV, lateral-line openings. Anterior on left. 14. Dorsal view of head $\times 1$. F, frontal component of supraorbital canal; JFD, junction of frontal canal with dermosphenotic; MP, median pore of supraorbital commissure; N, nostril; NA, nasal component of supraorbital canal. 15. Lachrymal bone $\times 5.3$. I-IV, lateral-line openings. Anterior on right; dorsal above. 16. Ventral view of head $\times 1.7$. D, dentary; JDA, junction of dentary with articular; P₁, preopercle; SO, subopercle; VM, ventral tip of maxilla.

from a cursory observation, for the anterior pores on the jaw of *Lepomis* open in very close approximation to the median suture; in *Cichlasoma* (Fig. 13) this same pore opens some distance behind this point.

The dermosphenotic or suborbital (post-orbital, auct.) number six (Fig. 7) communicates at its upper end with the common sinus behind the eye. This small bone, which rests in a groove on the sphenotic, is in direct contact at its ventral extremity with the dorsal end of a sub-orbital number five (Fig. 7). As is true in the remainder of the suborbital series, at their point of juncture the lateral walls of these two bones are sculptured, i. e., recessed away from each other, to form an oval foramen through which the external canaliculus extends out onto the skin (Figs. 12 and 14). Suborbital three and four are represented by a single bone with a foramen at its center and number two (jugal) communicates with its anterior opening. The jugal then makes connection with the postero-ventral opening of the lachrymal or suborbital number one. All of these bones often possess flat, wing-like processes extending parallel to the head surface.

The lachrymal (Fig. 15) is a fairly large, flattened, parallelogrammatic bone which bears two posterior openings, one dorsal and one ventral, and two anteriorly, dorsal and ventral. The edges of the bone, though often being slightly scalloped, are free of spination. There is a rather deep notch in the posterodorsal margin, and a slight groove, just posterior to the ventral opening, to receive the anterior end of the jugal (Fig. 15). The canal system is only slightly raised above the surface so that on gross inspection the bone appears quite smooth. On closer observation it can be seen that the areas around the canals have been secondarily ossified.

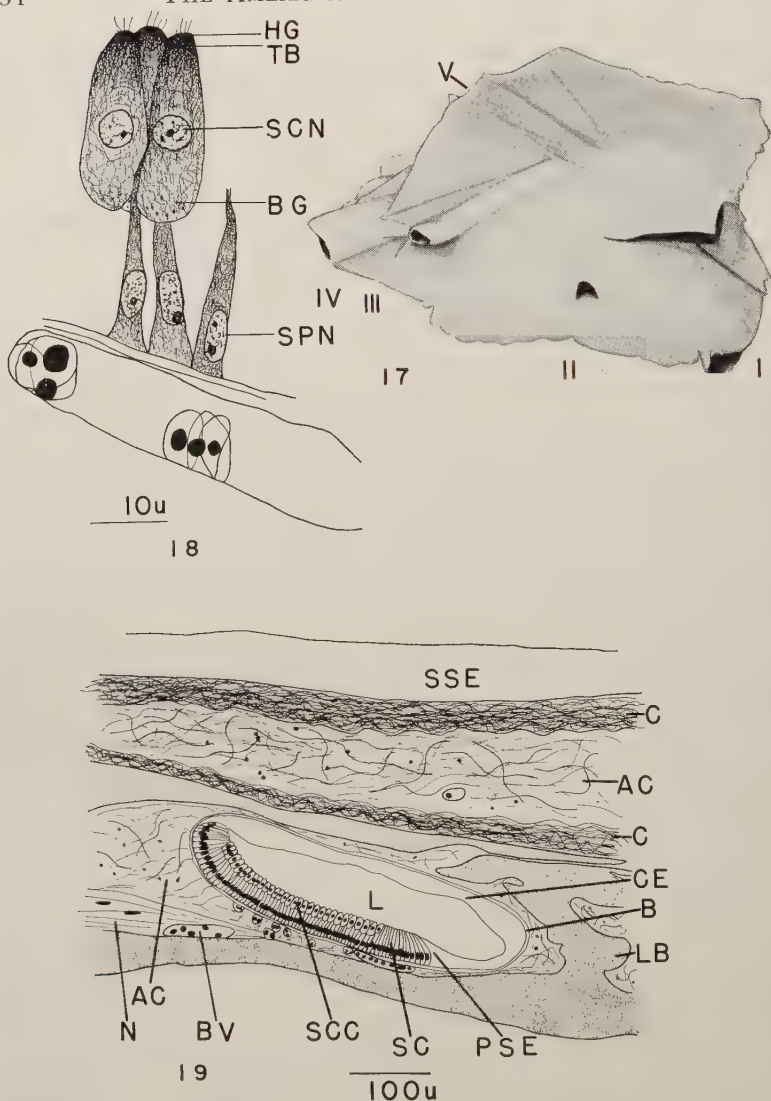
The suborbital series of *C. cyanoguttatum* is like that in some of the sunfishes, i. e., *Ambloplites rupestris*, etc., in possessing six ossicles and in being continuous from the postocular sinus to the lachrymal component. These are, however, several dissimilarities. In all of the specimens of *Cichlasoma* observed, the dermosphenotic, ossicles two, five and the compound three and four were always represented as completely tubular bones, i. e., no open spaces in their walls. In sunfishes their homologues are very often found as simple open channels or with their lateral walls barely touching in one or two small areas. There are, with few exceptions, no special openings for the exit of external canaliculi, the latter simply arising between the ends of the ossicles. The centrarchid jugal is very often lacking, in which case the infraorbital canal is incomplete. The only occurrence of a compound suborbital bone in sunfishes was seen after looking at several hundred individuals. This involved the jugal and suborbital number three in *Micropterus coosae*. However, this single occurrence is considered to be an anomaly and the bone does not in any way resemble the normally-occurring compound structure seen in *Cichlasoma*.

Another obvious difference between sunfishes and the Rio Grande Perch lies in the morphology of the first suborbital or lachrymal. In *Cichlasoma* the bone is elongated in a postero-anterior direction away from the eye and toward the snout, whereas in centrarchids, excluding *Elassoma*, the lachrymal is elongated in a dorsoventral direction and is usually curved on its posterior margin to fit the curvature of the eye. With a few exceptions it is spinous at its antero-ventral edge in the Centrarchidae and its over-all sculpturing is more complex than in the relatively much smoother cichlid bone.

The third lateral-line bearing skeletal component that communicates with the post-orbital sinus is the frontal bone (Figs. 11 and 17). This compact bone possesses five openings: one postero-lateral, one anterior, one above the eye, one near the nostril and one medio-ventral. It is strongly convex in all directions and bears a high crest along its inner edge. This crest is involved in the median suture for its entire length and depth (Fig. 11). The frontal lateral-line canal, after entering the bone from the sinus, progresses directly to the median plane where it bends anteriad, then continues forward until it communicates with the posterior end of the nasal. As it follows this path it gives off two branches, both completely enclosed in bone. One of these, designated II in Figure 18, is located above the eye, the other, marked III, opens just above the nostril. The latter tube is raised above the surface of the frontal and is supported by mesial and ventral struts of bone. The median opening is placed at the base of the bony crest (Fig. 11) from whence it is continued upward and forward by a groove in the crest. A similar groove occurs in the opposite frontal and when the two crests are in their normal sutured position a coronal tube is formed which opens to the exterior on the median line (Fig. 14). The foregoing explains why one is unable to discern the affinities of this pore from India-ink injected specimens.

There are few similarities between the frontals of *C. cyanoguttatum* and those of serranids or sunfishes. In most of the species of the latter two taxa, observed by this writer, there are only four openings in the lateral line and the canal itself is rather superficially placed on the frontal, its position and conformation being easily seen in injected specimens. In centrarchids there are no branches enclosed in bony tubes such as those illustrated in *Cichlasoma*. In sunfishes the frontal canal is a simple Y-shaped tube, the median arm of which opens near the midline, a similar canal opening from the opposite side of the head. An external canaliculus of connective tissue then arises and opens to form the coronal pore, which is a different situation than exists in *Cichlasoma*. Furthermore, the coronal pore of the Rio Grande perch is directed anteriad; in centrarchids it is directed strongly caudad.

The nasal (Fig. 1), the remaining bone of the lateral-line system, is situated anterior to the frontal and is completely ossified, i. e., there are no gaps in its walls. Its anterior and posterior ends are depressed,



Figs. 17-19.—Lateral line system of *Cichlasoma cyanoguttatum*. 17. Lateral view of frontal bone $\times 4.7$. I-V, lateral-line openings. Anterior on left; dorsal above. 18. Lateral-line sensory cells and associated structures (longitudinal section). BG, basal granule; HG, sensory-hair granule; SCN, sensory-cell nucleus; SPN, sustentacular-cell nucleus; TB, terminal bar. 19. Longitudinal section of the lachrymal bone and one of its contained neuromasts. AC, areolar connective tissue; B, basement membrane; BV, blood vessel; C, dense connective tissue; CE, cuboidal epithelium; L, lumen of lateral-line canal; LB, lachrymal bone; N, nerve; PSE, pseudo-stratified epithelium; SC, sustentacular cells; SCC, sensory cells; SSE, stratified squamous epithelium.

giving the bone an appearance of being bent in the middle, and the anterior half is deflected laterad, its tubular portion resting on the curved, plate-like component. The posterior opening, slightly raised above the surface of the bone and protected by osseous lamina above, communicates with the anterior-most opening of the frontal. The anterior pore of the nasal opens to the exterior near the snout tip.

As in its other lateral-line bones, the cichlid nasal is unlike that of any sunfish in which it is usually straightly-tubular, sometimes slightly laterally curved, and usually widened posteriorly to receive the canal of the frontal. Its dorsal wall is usually incomplete.

SENSE ORGANS OF THE SYSTEM

The formation of the lateral line must be completed at a relatively small size in this fish, because all of the canals were completely formed in a specimen 26 mm in standard length. As external neuromasts were not noted the following discussion will concern the neuromasts enclosed in canals.

The canal organ (Fig. 19) of *Cichlasoma* has the same general appearance of many other fish species (Moore, 1956; Moore and Burris, 1956) and is quite like that of most centrarchids (unpublished). The organ is a lozenge-shaped body, averaging $409.0\ \mu$ ($371.0\text{--}447.0$) in diameter, situated on the floor or proximal wall of the lateral-line canal, according to the location of a particular canal. The lateral-line tube enclosed by the bony housing is made up of a homogeneous substance which stains pale blue with Mallory's triple stain. Consequently, it is assumed that this substance is a type of connective tissue. This connective-tissue canal, which averages $507.4\ \mu$ ($500.5\text{--}514.3$) in diameter, is supported on all sides by loose areolar connective tissue in the bony canal (Fig. 19), the latter varying from 762 to $830\ \mu$ in diameter. The connective tissue tube is actually nothing more than the basement membrane of the epithelial cells lining the canal.

The neuromast consists of two types of cells (Figs. 18 and 19): the sustentacular cells and the sensory cells. The last named cells are completely surrounded by the supporting cells, their bases not touching the basement membrane, and are slightly depressed below the surface of the neuromast so that the organ is thicker in the region adjacent to the sensory area than at its center. The sensory area occupies approximately 55.5 per cent of the total surface area of the organ and averages $227.0\ \mu$ ($202.0\text{--}259.7$) in diameter. Typically (Fig. 18), the sensory cells are tenpen-shaped and measure $8.4\ \mu$ ($6.7\text{--}9.9$) at the base and $5.4\ \mu$ ($4.2\text{--}6.2$) at the apex. They are decidedly polarized, staining much more intensely at their apices than elsewhere. Apically, these cells bear from three to five sensory bristles or hairs, each of which is in contact with a minute, basophilic, blepharoplast-like granule located just beneath the cell membrane. The "hairs" average $2.18\ \mu$ ($1.7\text{--}3.2$) in length. It is usually stated (Sato, 1955; Bunker, 1897; Daget, 1949; and others) that each

sensory cell bears a single hair, but in *Cichlasoma*, and in the centrarchids (unpublished) thus far observed by me, the sensory hairs seem to be multiple. The nuclei of these cells are round, centrally placed, vesicular and average 5.1μ (4.0-5.9) in diameter. The nuclear walls are irregularly thickened by chromatin deposition and both acidophilic and basophilic nucleosomes, measuring 0.8 to 1.4μ in diameter, may be seen within it.

Near the apex the sense cells, which average 25.6μ (22.0-30.8) in length, proliferate well-developed terminal bars where they come into contact with their neighbors. Some small granules may be seen below the nucleus, but the basal filaments described by Moore (1956) in *Lepomis humilis* were not seen.

The sustentacular cells (Fig. 18) are very tall and slender, averaging 48.9μ (48.3-57.2) in length, with a finely granular cytosome that is lighter in its staining reactions than that of the sensory cells. The nuclei are oval, as is characteristic of such cells, and cause the cell to bulge in their proximity. These oval structures, like the sensory nuclei, are vesicular in appearance, average 3.5μ (2.9-4.2) in diameter, are basally placed, and bear acidophilic and basophilic endosomes 0.7 to 1.3μ (average 0.98) in size. The supporting cells, peripherally located in the organ, measure 2.3μ at their apices, at which point there are usually seen some terminal bars. In the sensory part of the organ these cells (in sections of 5.0μ thickness or less) are seen to penetrate upward between the sensory cells, their pathway becoming slightly tortuous because of deformation by the contours of the hair-bearing cells. A tangential section of the organ shows that at least the apical ends of the supporting cells, and perhaps the sensory cells as well, are connected by intercellular bridges. These same structures have been noted by Moore (1956) in *Lepomis*, Branson in centrarchids (unpublished), and Maximow and Bloom (1944) in several mammalian tissues. In the pigmy sunfish there is some indication that these bridges may extend throughout the length of the cells.

The general lining of the connective tissue canal is of a moderately high cuboidal nature with scattered goblet cells. However, near the neuromast (Fig. 19) this lining assumes a pseudostratified nature and the goblet cells become very numerous.

The cupula, which several authors have noted in other species (Denny, 1937; Dijkgraaf, 1952; and others) was not seen in this study. However, since this structure is easily dislodged, it may have been removed during fixation and/or staining.

Compared with the canal neuromasts in sunfishes, that of the Rio Grande perch is of greater diameter. Across the base of the organ, in the last named species, the average number of cells was found to be 142. The count in a similar area in representative centrarchids is as follows: *Lepomis auritus*, 85; *L. megalotis*, 53-65; *Acantharchus*, 75-80; *Centrarchus*, 85-90; *Chaenobryttus*, 125-135; and *Pomoxis*, 130-135. The cichlid neuromast is also slightly taller

than those of most centrarchids. Otherwise, this sensory structure is quite comparable in the two families of fishes.

INNERVATION

The innervation of the lateral-line organs is accomplished, as in other fishes (Holmgren, 1942; Hyman, 1956; Moore and Burris, 1956) by branches of the Facial (VII), Glossopharyngeal (IX) and the Vagus (X) nerves. Wherever a neuromast occurs, a nervous twig penetrates the bony canal and the connective tissue surrounding the organ; the twig enters the organ at about its basal center and splays out around the bases of the sensory cells. I could not see any indication of an intimate contact between the sense cells and the nervous endings. However, special techniques would be required to demonstrate this. These nervous twigs are myelinated to the point where they enter the organ and appear to lose their sheath at this junction.

Because of the peculiar form of the lateralis, i. e., the conspicuous line on the trunk of the body, some dissections were made to determine the mode whereby the neuromasts of the lateralis receive their nerve branches from the Vagus, which becomes superficial near the middle of the upper one-third of the supracleithrum, from whence it sends branches to the short canal in the post-temporal, supra-temporal-intertemporal, lateral-extrascapular and a long branch, the lateralis Vagus, caudad in the horizontal skeletogenous septum as observed in other species (Rode and Raband, 1926). The latter branch gives off a twig to each neuromast in the trunk line. As the lateralis canal curves dorsal and away from the septum, these branches become progressively longer, then shorter as the line begins to slope back toward the septum. At the junction where the lateralis is interrupted the twigs cease to be formed and take up again where the second line begins. The nerve twigs to the lateral-line organs of the caudal peduncle, however, are quite short because in this region the Vagus lateralis directly underlies the lateral-line canal. It would be informative to study the embryonic development of this portion of the lateral-line in *Cichlasoma*, but this was not possible in this study. As pointed out above, the smallest specimen available was only 26 mm in standard length and its canal system was already completed.

CONCLUSION

Cichlasoma cyanoguttatum is a member of a depauperate fauna in the United States and though it occupies a similar type of habitat, it is obviously not very closely related to the Centrarchidae. From a gross survey of the lateral-line system in the Rio Grande perch it appears that the morphology of this system is nearly identical to its homologue in sunfishes and serranids, the peculiar form of the lateralis canal excepted. Upon closer inspection, especially of the osseous components of the system, it becomes obvious that there are con-

siderable differences between the two last mentioned families and the system in *Cichlasoma* as regards their lateral lines.

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Revision of the Genus *Melanactes*, with a Proposed New Genus (Coleoptera, Elateridae)¹

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ABSTRACT: The present revisional work of the genus *Melanactes* defines the limits of its six species and presents some ideas regarding their relationships. The distribution of this genus is principally in the United States. Three of the species occur throughout the central and eastern part of the country. One species is confined to the central part and another to the East Coast. Finally, one species occurs in south Oregon, California, and northern Baja California (México). One species is placed under synonymy and another is transferred to a new genus herein described, the latter species occurring only in the southern part of Arizona. A key to species is presented, and redescription of all species are made. Some suggestions concerning the phylogenetic position of the genus *Melanactes* and the new genus are also given.

INTRODUCTION

Melanactes is a small genus of the family Elateridae or click-beetles. Adults of the genus are large, black, shiny beetles found in or near woody areas, frequently resting on the bark of tree trunks. Larvae are very rarely collected, and only the larva of *M. densus* has been associated with its adult. Since the life cycle, at least of *M. densus*, is very long, it is unlikely that the larvae of the genus are predaceous. Rather, they probably feed on decomposing woody material.

The genus, endemic to North America, is represented by six species. Previously, eight species were listed but in the present study one of these is assigned to a new genus and another is placed in synonymy.

The classification of the species of the genus *Melanactes* has been in a confused state for a long period of time. As in many genera of Elateridae, its species do not have striking morphological differences; for example, even the male genital organs, which in the majority of beetles provide very useful characters for the separation of species, are essentially uniform throughout the genus. Moreover, no one has previously attempted to study the species critically, using all of the material available in museums and private collections.

The results of the present study have permitted me to make improved definitions of the species as well as to draw conclusions regarding their phylogenetic relationships. In particular, good interspecific differences have been found in the female organs of reproduction. Externally, useful characters include those of the sculpturing

¹ Submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology in the Graduate College of the University of Illinois, 1960.

and setation of the pronotum and elytra, proportions of the pronotum, and total length.

Acknowledgments.—I wish to acknowledge with gratitude the generous assistance of the following institutions and individuals in providing me with the material and information upon which the present revisionary study is based: American Museum of Natural History, J. C. Pallister; California Academy of Sciences, H. B. Leech; Carnegie Museum, G. Wallace; Canadian National Collection, E. C. Becker; Chicago Natural History Museum, R. L. Wenzel; Cornell University, H. Dietrich; Illinois Natural History Survey, M. W. Sanderson; Iowa State College, J. L. Laffoon; North Carolina State College, W. M. Kulash; Oklahoma State University, W. A. Drew; Ohio State University, J. N. Knull; Purdue University, L. Chandler; University of Arizona, F. G. Werner; University of California (Berkeley), J. A. Powell; University of California (Davis), A. T. McClay; University of Florida, T. J. Walker; University of Illinois; University of Kansas, G. Byers; University of Missouri, W. R. Enns; University of Nebraska State Museum, R. E. Hill; United States National Museum, J. F. Gates Clarke; Utah State University, G. F. Knowlton; Washington State University, M. T. James.

I am very much indebted to M. C. Lane for suggesting the problem, for the loan of material, and for information. I am also indebted to E. C. Becker for his valuable suggestions and for his interest in my work. For the loan of the type specimen of *Pseudomelanactes agrypnoides* I want to thank H. B. Leech. For comparing my material with the LeConte type material of *Melanactes* I am grateful to F. Pacheco.

My study at the University of Illinois was made possible by a scholarship from the Rockefeller Foundation. For their interest in me and their assistance I am grateful to a number of individuals associated with the Foundation, both in Mexico and in New York. In particular, I want to mention D. Barnes, W. W. Gibson, J. J. McKelvey and K. Wernimont.

Finally, I take pleasure in thanking R. B. Selander for his advice and direction in the course of this study.

HISTORICAL REVIEW

The taxon now known as the genus *Melanactes* was first defined by Germar (1843), who segregated *M. piceus*, *M. morio*, and *M. reichei* as a separate division of the genus *Pristilophus* Latreille. It was elevated to generic rank by LeConte (1853) in his revision of the Elateridae of the United States. LeConte included 7 species in the genus, of which 2 were described as new in the same publication. The characters given by LeConte for *Melanactes* are as follows: tarsi provided with a very dense brush of hairs beneath; pubescence not conspicuous above; mesosternum elevated, forming a ridge at the sides of the mesosternal groove; pronotum strongly margined at the sides, with the hind angles strongly carinated at the base, and with 2 teeth in front of the scutellum.

Candèze (1863), in his *Monographie des Elatérides*, placed *Melanactes* in his second group (called *Melanactites*), along with 6 other genera. In 1891 he revised his earlier classification, recognizing 27 tribes. In this new classification the group *Melanactites* was broken up and the genus *Melanactes* was placed in the tribe, Corymbi-

tites. This system was followed by Schwarz (1906) in cataloguing the family Elateridae in the Genera Insectorum.

Working only with the nearctic elaterids, Hyslop (1917) modified the classification of the family considerably as a result of his studies of both larval and adult characters. He recognized 4 subfamilies and 10 tribes. He could not determine the precise position of *Melanactes* in his classification because the larva of the genus was unknown to him. However, on the basis of adult characters he was able to assign it to the subfamily Pyrophorinae. This assignment was accepted by Leng (1920) although he placed it in a separate tribe (Melanactini) of Pyrophorinae.

Subsequent workers have accepted Hyslop's assignment. More recently, Glen (1950) had the opportunity of studying a larval specimen of *M. densus*. As a result of his study, he assigned *Melanactes* to the pyrophorine tribe Denticollini (=Lepturoidini), although he noted that the larva of the genus is quite distinct morphologically from the other members of the tribe.

The limits of the genus have not changed since LeConte's time. One species (*M. agrypnoides*) was added to the genus by Van Dyke in 1932, but in the present study this species is transferred to a new genus.

CLASSIFICATION

Genus *Melanactes* LeConte

Melanactes LeConte (1853, p. 493).

Description.—The members of this genus are rather large insects, measuring from 15 to 33 mm in length. Their main morphological features are as follows:

Body robust, elongated, subdepressed, shiny or very shiny. Color black or reddish-black, the legs and venter dark red, always a little lighter in color than the rest of the body. Mandibles directed forward. Antennae dark, with the apical segments sometimes becoming reddish-brown. Front depressed, sparsely punctured at the middle and posteriorly, becoming more densely and conspicuously punctured anteriorly and at the sides. Antennae serrate; second segment shorter than the third; these two segments not at all serrate, fourth to tenth segments moderately serrate, more or less alike in shape and in size; eleventh segment slightly longer than tenth and constricted at apex (Figs. 11-13). Pronotum as long as broad (measured at the middle), but generally appearing longer than broad, tapering gradually toward the head, with the widest point at the hind angles; pronotum strongly margined at the sides, the margin fading anteriorly at the middle; carina very prominent; hind angles almost parallel at the tip; basal part of the disc visibly sulcate; punctures variable. Elytra at base as broad as base of pronotum; elytra often broader at apical third than at base, especially in females; striae and interstriae variable, but always more strongly impressed at base and at sides than elsewhere. Scutellum heart-shaped, with pubescence variable. Prosternum vari-

ably punctate; prosternal spine very strong, wedge-shaped, with tip rounded; laterally and apically the spine is expanded to form a ventral shelf; height of spine more or less equal to distance between the fore coxae; surface of spine smooth and shiny. Mesosternum with sides of groove prominently raised, slightly divergent, deflected in front to form a short plate; mesepisterna and mesepimera clothed with yellowish hair of variable density. Metasternum smoother and more shiny than the rest of sternum; mesepisterna usually more distinctly punctate than metasterna. Hind coxal plates gradually narrowing toward metepisterna. Tarsi provided beneath with a dense golden brush of hairs; first segment almost twice as long as second; rest of segments gradually shorter; fifth segment as long as first. Tarsal claws simple. Abdomen finely, uniformly, and shallowly punctate.

Male genitalia (Figs. 5-8) with aedeagus elongate-triangular; parameres each with a large tooth laterally near apex, and with three or four setae at apex; basal piece quadrate.

Female genitalia (Figs. 14, 15, and 17) with a large bursa copulatrix, which has two or four heavy rows of spines internally; colleterial glands absent; two accessory glands present near anterior end of bursa copulatrix; spermathecal duct constricted near its junction with spermatheca.

Larva.—The only species of the genus known in the larval stage is *M. densus*. Glen (1950) described this larva from a specimen reared from eggs laid in captivity. It measured 38 mm at 5 years of age. Its main structural features are as follows: dorsum golden brown, venter paler; lateral membranes large, creamy white; caudal notch large, transverse; urogomphi short, robust, bifid; tergal prongs corniform, with sharp, upturned tips; outer prongs three or four times as long as the inner ones.

Discussion.—There is a sexual dimorphism in body size in the species of *Melanactes*. Generally speaking, females are larger than males and more robust in appearance.

The male genitalia are fairly similar in all species. The female genitalia exhibit some interspecific differences, among which the most useful are the number and arrangement of the rows of spines in the bursa copulatrix.

The type species of *Melanactes* is *M. densus* LeConte, as designated by Hyslop (1921).

Key to Species of *Melanactes*

1. Oregon, California, and Baja California Norte; surface of the scutellum without hairs; pronotum quadrate, coarsely and densely punctate, the punctures becoming confluent anteriorly and laterally; elytral surface shagreened throughout (under high magnification) *densus*
- Central and eastern United States; scutellum with hair on the surface; without the above combination of characters 2
2. Pronotum finely and uniformly punctate, each puncture bearing an appressed seta which is at least as long as the distance between punctures; pronotum with sulcus well marked at basal third and with a distinct im-

pression on each side at base of hind angle, parallel to carina; form narrower and more elongate than in other species; bursa copulatrix with two rows of spines (Fig. 17); extreme eastern and southeastern United States (Mississippi to Georgia, north to Maryland and Pennsylvania)

.....*reichei*
Pronotum more irregularly punctate, without setae or with very minute erect ones; pronotal sulcus and impressions weakly marked to obsolete; form more robust 3

3. Elytral striae at base well-marked, on disc not canaliculate but represented only by a row of shallow small punctures; interstriae flat, feebly rugose, and therefore very shiny; bursa copulatrix with four rows of spines; the spines very numerous (Fig. 15)*piceus*
Elytral striae canaliculate and well-marked for their entire length; interstriae feebly to strongly convex 4

4. Elytral striae deep, with deep punctures; interstriae strongly convex; bursa copulatrix with two rows of spines.*morio*
Elytral striae shallower; interstriae feebly to moderately convex; bursa copulatrix with four rows of spines 5

5. Pronotum flattened (lateral view), appearing longer than broad; elytral interstriae nearly flat; bursa copulatrix with relatively few spines in the median pair of rows; central, and central eastern United States; allopatric with *consors* (see Fig. 3)*puncticollis*
Pronotum convex, appearing more nearly quadrate; elytral interstriae moderately convex, deeper punctures on the striae; bursa copulatrix with numerous spines in the median pair of rows (much as in *piceus*); Kansas and Oklahoma.*consors*

Melanactes densus LeConte

Melanactes densus LeConte (1853, p. 494).

Melanactes schaumii Candèze (1865, p. 14).

Description.—Male. Length 17.5 to 24.5 mm; width 4.5 to 7.5 mm. Color black or reddish black, not very shiny. Head densely punctate at sides. Antennae with the serrate segments slightly longer than wide about two-thirds as long as pronotum (from apex to tip of hind angles). Pronotum slightly longer than wide, slightly convex; posterior angles not at all divergent; carina very broad and well raised, sides more or less parallel, rounded from the anterior third to front; disc moderately densely and finely punctured, the punctures becoming confluent and larger on the sides and very dense anteriorly; sulcus obsolescent or obsolete. Scutellum with surface glabrous except for some scattered yellowish hairs on the sides. Elytra feebly shiny; striae indicated only by rows of punctures that are separated from each other by approximately twice their diameter; intervals flat, the entire surface shagreened (under high power). Venter more shiny than dorsum. Proepisterna heavily punctate. Metasterna finely and shallowly punctate. Genitalia (Fig. 7) proportionally broader than in the other species but otherwise morphologically identical.

Female. Length 18.5 to 27.0 mm; width 5.5 to 8.5 mm. Pronotum very often as wide as long. Genitalia (Fig. 17) with two rows of spines in the dorsal part of the bursa copulatrix and a narrow row on each side.



Fig. 1.—Geographic distribution of *Melanactes densus* in California and Baja California Norte.

Distribution.—As can be seen in Figure 1, *M. densus* occurs in California and the extreme northern part of the peninsula of Baja California. In addition, I have seen a single specimen, without precise locality data, from Oregon. In California the species occurs throughout the state except that it avoids the Central Valley and the Mojave Desert.

The species has been collected from late February to early August, but mainly in April, May and June.

MEXICO: BAJA CALIFORNIA NORTE: San Pedro Mártir Mountains, 1.

UNITED STATES: CALIFORNIA: State label, 28; Ahwahnee, 1; Alameda, 1; Alameda Co., 2; mountains back of Alma, 1; Alma, Santa Clara Co., 1; Alpine, 1; Arpia, San Mateo Co., 1; Arroyo Seco Camp, Monterey Co., 4; Bass Lake, Madera Co., 1*; Beatrice, 1; Berkeley, 14; Big Pine, Inyo Co., 11*; Big Trees, Calaveras Co., 1; Bolinas, 1; Boonville, 1; Butte Creek, Butte Co., 6; Caliente, Kern Co., 1; Calistoga, 1; Camino, Eldorado Co., 2; Carmichael, 1; Casalona, 1; Castle Rock, Shasta Co., 1; Chester, Plumas Co., 2; Chicago Park, 1; Chile Bar, Eldorado Co., 1; Chino Canyon, 1; Chiquito, Madera Co., 1; Claremont, 5; Clarksburg, 2; Clear Creek, San Benito Co., 1; Clear Lake, Lake Co., 1; Coalinga, Fresno Co., 1; Colma, 1; Coloma, 2; Contra Costa Co., 1; Cottonwood Creek, Kern Co., 4; Courtland, 1; Cypress Ridge, Marin Co., 1; Danville, 1; Davis, 9; Dos Palos, 1; Eldorado Co., 2; Fairfax, Marin Co., 1; Fair Oaks, 2; Folsom, 1; Fresno, 3; General Grant National Park, 1; Glen Ellen, 1; Grass Valley, 1; Groveland, 2; Half Moon Bay, 1; Havilah, 1; Hayward, 1; Hemet Reservoir, San Jacinto Mts., 1; Hobergs, Lake Co., 1; Holy City, 1; Hot Springs, Tulare Co., 2; Huntington Beach, 2; Independence, Inyo Co., 2; Isabella, 1; Kaweah, Tulare Co., 14*; Kings River Canyon, 3; La Grange, 18; Lagunitas, Marin Co., 1; Lakeside, 1; Lindsey, Tulare Co., 4; Little Lake, 1; Lloyd Mead, 1; Lodi, 2; Loma Linda, 1; Lonepine, Inyo Co., 5; Los Altos, 4; Los Angeles, 4*; Los Gatos, 4; Mariposa Co., 1; Martinez, Contra Costa, 1; Marysville, 1; Mazourka Canyon, Inyo Co., 1; Meadow Valley, Plumas Co., 1; Miami Ranger Sta., Mariposa Co., 3; Michigan Bar, Sacramento Co., 2; Mission Valley, 1; Mohawk, 4; Mojave Desert, 1; Mokel Hill, Calaveras Co., 18; Mokelumne Hill, 2; Moss Beach, San Mateo Co., 2; Murphys, 2; Mt. Pinos, Kern Co., 2; Mt. View, Santa Clara Co., 1; Napa Co., 6; Natama, 1; Nelson Camp, Tulare Co., 1; Nevada City, 5; Northfork, 4; Oak Creek, Kern Co., 1; Oakhurst, Madera Co., 1*; Oakland, 1; Oakland Hills, 5; Orange Valley, 4; Oro Grande, 2; Outlet, 1; Owens Lake, 1; Oxnard, Ventura Co., 2*; Pacheco Pass, Santa Clara Co., 1; Palm Springs, 1; Palo Alto, 2; Paraiso Springs, 1; Pasadena, 2; Paso Creek, Kern Co., 1; Perkins, 2*; Pescadero, 1; Piedmond, 2; Pilot Hill, Eldorado Co., 1; Piris, 1; Placer Co., 1; Pleasanton, 1; Pleyto, Monterey Co., 1; Pomona, 1; Poso Creek, Kern Co., 1; Potwisha, 2; Poway, San Diego Co., 2; Quincy, 4 miles west, Plumas Co., 5; Redwood, 1; Richmond, 1; Riverside, 4; Round M. Giant Forest, 1; Rutherford, 2; Ryde, 1; Sacramento, 8*; Saint Bruno Hill, 3; Salinas, 1; San Anselmo, 1; San Diego, 8; San Francisco, 5; San Jacinto, 1; San Joaquin, 1; San José, 15*; San Leandro, 1; San Luis Obispo, 2; San Mateo, 1; Santa Bárbara, 5; Santa Cruz, 2; Santa Cruz Mountains, 2; Santa Monica Mountains, 1; Santa Paula, 2; Sequoia National Park, 21*; See Can, 5; Shasta Co., 3; Sierra Nevada, 1; Snowhine

* Records of this and other species followed by an asterisk were received (*in litt.*) from Mr. M. C. Lane.

Camp, Eldorado Co., 2; Soquel Creek, Santa Cruz Co., 3; Springville, 3; Stockton, 2; Strawberry, 1; Tejon Canyon, Kern Co., 6; Temecula, 1; Tin Rice, Amador Co., 1; Towle, 2; Trinity Co., 1; Trona, 6; Truckee, 1; Tulare Co., 6; Tuolumne Co., 7; Upper Lake, 1; Victorville, 9; Vina, 2; Visalia, 1; Walnut Grove, 3; Walnut Creek, Contra Costa Co., 1; Walker Pass, Kern Co., 2; Warners, 1; Watsonville, 4; Wanona, Mariposa Co., 2; Woody, 1; Yermo, 5 miles north east, 2; Ynez, 1. OREGON: State label, 1.

Discussion.—This species is the most distinct of all the species of *Melanactes*. It differs from the rest in having little or no pubescence, stouter antennae (Fig. 12), and a more coarsely and densely punctate pronotum. In addition, the body surface is less shiny.

M. densus is the only species of this genus that is known in the larval stage (see above).

The type series of *M. densus* consists of 8 specimens in the LeConte collection at the Museum of Comparative Zoology at Harvard. The first specimen, which bears LeConte's golden locality disc (California), is labeled as Type No. 2619; it measures 23 mm in length and 7 mm in width. One specimen has an identification label reading "*Melanactes schaumii* Cand." Candèze (1863) himself recognized *M. schaumii* as a synonym of *M. densus*; his type is deposited in the British Museum of Natural History.

Melanactes reichei (Germar)

Pristilophus reichei Germar (1843, p. 85).

Description.—Male. Length 20.5 to 21 mm; width 5.0 to 5.5 mm. Body elongated, appearing more slender and more depressed than the rest of the species. Color shiny black to dark red-brown. Front with scattered, well-impressed punctures. Pronotum longer than wide, very flat, tapering gradually toward front; sulcus on the basal third well impressed; at base of hind angles a more or less elongate impression is present; surface densely punctate, especially in front and on the sides, covered with tiny appressed setae. Elytra elongate, tapering from middle to apices; striations and punctures distinct; interstriae slightly convex, more distinctly rugulose than in *M. piceus*. Mesosternum and anterior part of metasternum strongly and closely punctate, covered with a pile of yellowish hairs. Abdomen finely and uniformly punctate throughout. Genitalia elongate; parameres more rounded at the tip than in the other species (subtle difference).

Female. Length 21 to 28 mm; width 5.0 to 7.0 mm; generally larger than male. Bursa copulatrix with fewer spines than in the other species, with the lateralmost row of spines on each side reduced to very few spines.

Distribution.—The geographic distribution is shown in Figure 2A. This insect has been collected from April to July.

GEORGIA: Atlanta, 1; Clayton, 1. MARYLAND: College Park, 1; Hyattsville, 1; Jackson's Island, 3; Montgomery Co., 2; Odenton, 1; Plummers Island, 13. MISSISSIPPI: Lucedale, 2. NORTH CAROLINA: Julian*; Murphy, 2; Raleigh, 3; Tryon, 1. PENNSYLVANIA: Jeannette, 1. SOUTH CAROLINA: Clemson College.*

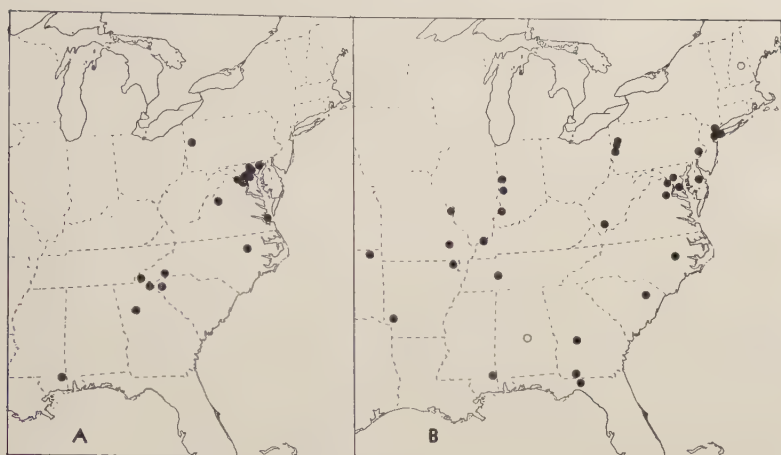


Fig. 2.—Geographic distribution of *Melanactes reichei* (A) and *Melanactes morio* (B).

VIRGINIA: State label, 1; Difficult Run, 1; Glen Carlyn Alex. Co., 2; Great Falls, Fairfax Co., 4; Nelson Co., 1; Phoebe, 1. WASHINGTON, D. C.: 1.

Discussion.—Two extreme variants of this species should be mentioned. These are females collected in Lucedale, Mississippi. They are lighter reddish-brown than usual and have more spines in the bursa copulatrix than in other females. Otherwise, they agree with the other specimens.

I have noticed that the species *Ctenicera aethiops* Herbst has been frequently misidentified as *M. reichei*. The two are similar only in general appearance.

The type is presumably in the Zoological Museum of Berlin.

Melanactes morio (Fabricius)

Elater morio Fabricius (1798, p. 138).

Elater lacunosus Fabricius (1801, p. 224).

Description.—Male. Length 19.5 to 26.5 mm; width 6 to 7.5 mm. Robust, very much of the size and form of *M. piceus*. Pronotum slightly convex; punctures variable, from shallow to deep, sometimes confluent; sulcus visible in the basal third. Elytra having the striae deeply canaliculate, with deep punctures; interstriae very convex, (slightly rugulose) with scattered punctures throughout. Venter as in *M. piceus* but generally with better marked punctures. Genitalia as in *M. piceus*.

Female. Length 22 to 30 mm; width 6 to 9 mm; generally larger than male. Punctures of pronotum sometimes more distinct than in male. Genitalia with two long rows of spines in the bursa copulatrix, more or less as in *M. densus*.

Distribution.—The geographical distribution of this species is

shown in Figure 2B. The species has been collected from May to July.

ALABAMA: State label, 2. ARKANSAS: Hempstead Co., 1; Laurence Co., 1. DELAWARE: State label, 2. FLORIDA: State label, 2; Monticello, 1. GEORGIA: Chakri, 1; Ft. Valley, 2; Thompson Mills, 1. ILLINOIS: Catlin, Camp Drake, 1; Mt. Carmel, 1; Metropolis, 1. INDIANA: Parke Co., 1; Vigo Co., 1. MARYLAND: State label, 1; Beltsville, 1; Jackson's Island, 1. MISSISSIPPI: Lucedale, 1; Meridian, 1. MISSOURI: St. Louis, 1; Williamsville, 4. NEW HAMPSHIRE: State label, 2. NEW YORK: State label, 4; New Windsor, 1; Staten Island, 1; West Point, 3. NEW JERSEY: State label, 1; Da Costa, 1; Fort Lee, 1; New Egypt.* NORTH CAROLINA: State label, 1; Climax*, Julian*; Raleigh, 3. OKLAHOMA: Blue Jacket, 1. PENNSYLVANIA: Fayette Co., 2; Jeannette, 2; Lingsletown, 1; Millvale, 1; Philadelphia Co., 1. SOUTH CAROLINA: State label, 2; Florence, 2. TENNESSEE: State label, 1; Benton Co., 1. VIRGINIA: Arlington, 1; Clarendon, 1; Fredericksburg, 1. WEST VIRGINIA: West Sulfur, 1.

Melanactes puncticollis (LeConte)

Pristilophus puncticollis LeConte (1852, p. 68).

Description.—Male. Length 17.5 to 25 mm; width 4.5 to 6.0 mm. Color black to dark reddish black, somewhat shiny. Head sparsely punctate on anterior part, almost glabrous at middle. Pronotum appearing longer than wide; disc flat; sulcus shallowly marked at basal third; more dense on front and at the sides than on disc; some punctures bearing a small erect hair (visible only under high magnification). Scutellum densely pubescent. Elytra elongate; stria well-

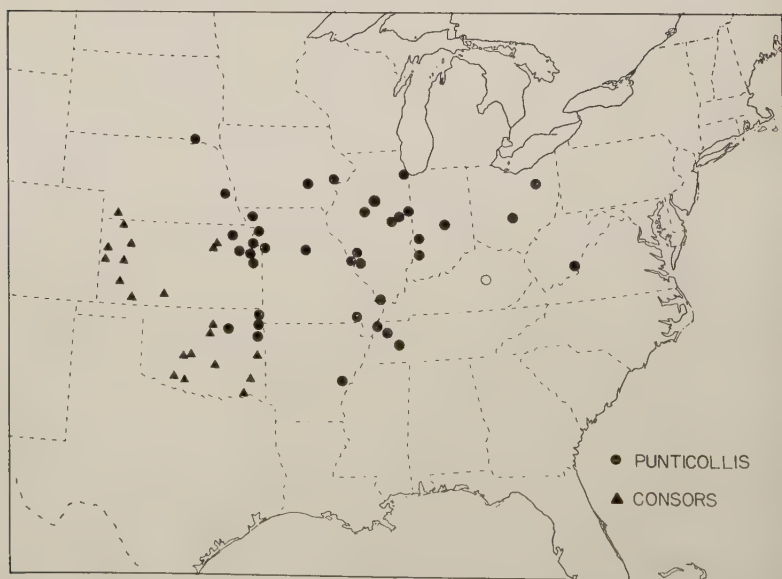


Fig. 3.—Geographic distribution of *Melanactes puncticollis* and *Melanactes consors*.

marked at base, elsewhere only faintly canaliculate, represented by punctures which are separated from each other by their own diameter; first three interstriae flat, the rest becoming very slightly convex; interstriae punctate and to some extent rugulose. Genitalia as in *M. piceus*.

Female. Length 21 to 24 mm; width 5 to 6.5 mm; usually larger than male. Genitalia as in *M. piceus*, except for the short median rows of spines in the bursa copulatrix, which have fewer spines.

Distribution.—The geographical distribution is indicated in Figure 3. Specimens have been collected from late April to August but mostly in June.

ARKANSAS: State label, 9; Prairie Co., 1. ILLINOIS: State label, 2; Alton, 1; Belle Smith Spring, Pope Co., 2; Falling Springs, 1; Goodfield, 6; Havana, 1; Mascoutah, 1; Monticello, 4; Plainfield, 1; Pulaski, 1; Urbana, 5; Vermilion Co., 1. INDIANA: Knox Co., 1; Marion Co., 1; Vigo Co., 2. IOWA: Iowa City, 1; Ames, 1. KANSAS: State label, 4; Douglas Co., 4; Lawrence, 3; Leavenworth Co., 1; Onaga, 3; Topeka, 1. KENTUCKY: State label, 2. MISSOURI: State label, 1; Columbia, 3; Kansas City, 1; Maryville, 1; Saint Joseph, 1; Saint Louis, 4; Webster Groves, 1; Williamsville, 1. NEBRASKA: South Bend, 1; West Point, 1. OHIO: State label, 1; Columbus, 2; Ira, 1; Wayne Co., 1. OKLAHOMA: Ottawa Co., 1; Sallisaw, 1; Tahlequah, 1; Tulsa, 1; Wyandotte, 1. SOUTH DAKOTA: Springfield, 2. TENNESSEE: Dyer Co., 1; Lake Co., 1; Perryville, 1.

Discussion.—This species resembles *M. piceus* but can be separated easily by its smaller size and by the distinctness of the striations of the elytra. It is also very similar to *M. consors*. It can be separated from the latter on the basis of its less convex pronotum and allopatric distribution.

The LeConte material consists of seven specimens, two of which are labeled "Ks." A specimen bearing a label reading "Type No. 2620" is the smallest of the series (length 20 mm; width 6 mm). LeConte gave the type locality as Missouri Territory.

Melanactes consors LeConte

Melanactes consors LeConte (1853, p. 495).

Description.—Male. Length 17.5 to 23 mm; width 5 to 6 mm. Similar to *M. puncticollis*. Head moderately densely and more or less deeply punctate, the punctures at front more numerous and deeper than elsewhere. Pronotum as wide as long; disc convex; surface with a continuous convexity from base to front; sides rounded; hind angles parallel; sulcus barely visible on the posterior third. Elytra broad; striae distinctly canaliculate, with well impressed punctures; interstriae semiconvex, distinctly rugulose. Genitalia as in *M. puncticollis*.

Female. Length 20.5 to 28 mm; width 6 to 8 mm; generally larger than male. Pronotum wider than in male. Genitalia as in *M. piceus*.

Distribution.—The general distribution is shown in Figure 3. The species has been collected from May to August, mostly in June.

KANSAS: State label, 6; Belvidere, Kiowa Co., 1; Decatur Co., 1; Garden

City, 1; Gove Co., 9; Greeley, 1; Manhattan, 1; Riley, 2; Scott Co., 4; Wallace Co., 3. NEBRASKA: McCook, 1. OKLAHOMA: Hinton, 1; Hugo, 1; Kiowa, 1; Norman, 2; Pawnee, 2; Pearson, 1; Stillwater, 1; Wichita National Forest, 4.

Discussion.—This is the smallest species of the genus. It was described from one specimen collected in Nebraska. This specimen, which is in the LeConte collection at the Museum of Comparative Zoology, bears type label No. 2621. It measures 24 mm in length and 8 mm in width.

Melanactes piceus (DeGeer)

Elater piceus DeGeer (1775, p. 162).

Elater laevigatus Fabricius (1798, p. 138).

Pristilophus femoralis Melsheimer (1844, p. 216).

Melanactes procerus LeConte (1853, p. 493) *New synonymy*.

Description.—Male. Length 21 to 28.5 mm; width 5.5 to 7.5 mm. Body robust, subdepressed, color black or dark reddish black, very shiny. Antennae and legs reddish black, somewhat lighter in color than body. Pronotum appearing longer than wide; hind angles slightly divergent; punctures sparse and very shallowly marked, so that the surface appears almost smooth. Elytra as wide as base of pronotum; striae on disc not at all impressed, indicated merely by rows of elongate punctures; striae at sides a little better impressed; all striae finely punctate, the punctures separated from one another by more than their length; interstriae flat, very minutely and indistinctly punctulate; interstrial rugosity feeble. Scutellum covered with a

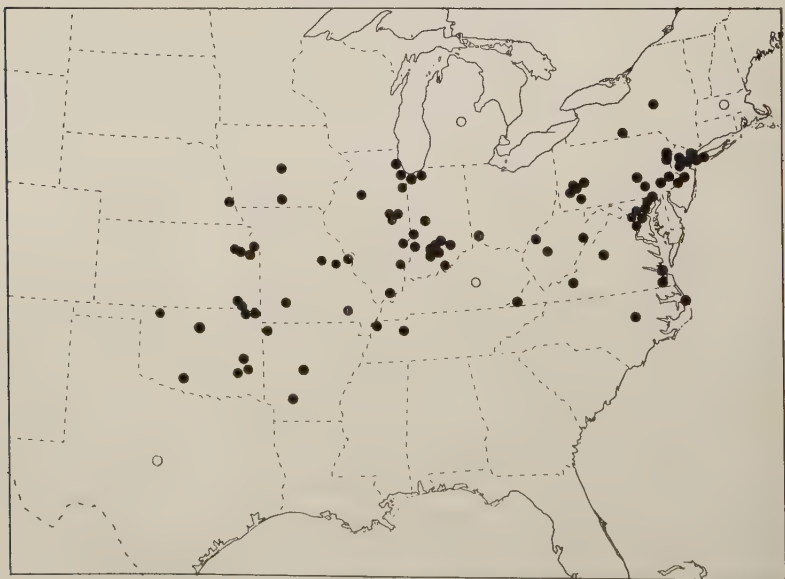


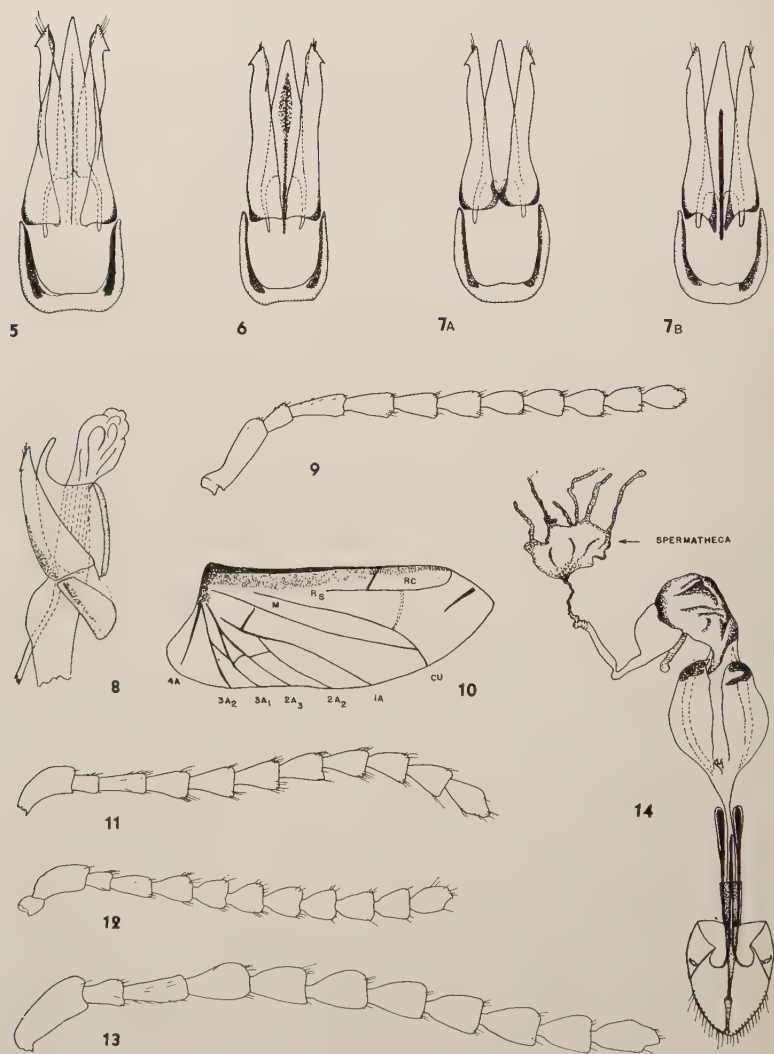
Fig. 4.—Geographic distribution of *Melanactes piceus*.

dense pile of yellowish hair. Mesepisterna and mesepimera covered with yellowish hair. Genitalia (Fig. 5) slightly longer and more slender than the general type.

Female. Length 20.5 to 33 mm; width 4.5 to 9 mm; usually larger more robust than male. Body more heavily punctate than in male; in some extreme variants the punctures of the pronotum become confluent at the sides. Genitalia (Fig. 15) with numerous spines in the bursa copulatrix arranged in a pair of heavy lateral rows running to the front and four dorsal rows, the median pair of which are much shorter than the others.

Distribution.—The general distribution of *M. piceus* is indicated in Figure 4. The species has been collected from early April to August, but mainly in May and June.

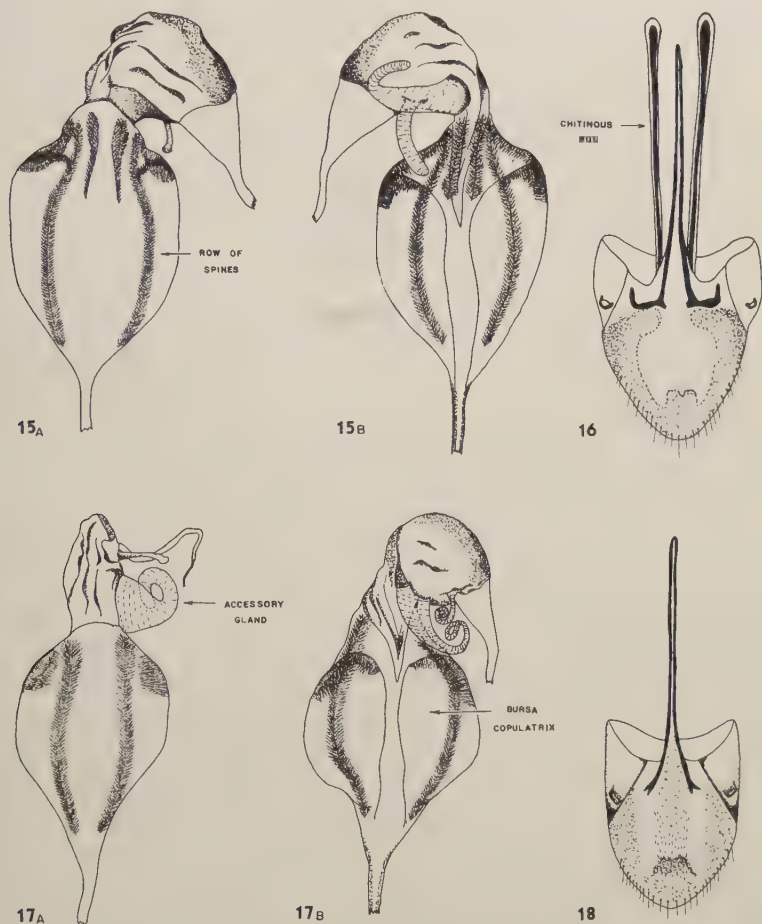
ARKANSAS: State label, 2; Hot Springs, 1; Washington Co., 2. ILLINOIS: State label, 13; Beebe's Woods, east of Crete, 1; Cabelen, 1; Chicago, 3*; Downers Grove, 2; Falling Spring, 1; Galesburg, 1; Homewood, 1; Mahomet, 4; Mascoutah, 1; Monticello, 3; Oakwood, 3; Oblong, 2; Parkersburg, 1; Peoria Co., 1; Pinkstaff, 1; Putnam Co., 1; Saint Joseph, 2; Urbana, 7; White Heath, 2; White Springs, 1; Willow Springs, 16*. INDIANA: Brown Co., 1; Clark Co., 17; Crawford Co., 3; Dune Park, 2; Harrison Co., 1; Henryville, 1; Jacks Co., 1; Jennin Co., 1; Knox Co., 1; Lake Co., 1; Lawrence Co., 1; Putnam Co., 2; Valparaiso, 1 Vigo Co., 1. IOWA: State label, 3; Ames, 5; Carbonado, 1; Leon, 1. KANSAS: State label, 20; Bourbon Co., 1; Douglas Co., 4; Elk City, 1; Lawrence, 1; Leavenworth Co., 2; Montgomery Co., 2; Topeka, 2. KENTUCKY: State label, 3. MARYLAND: State label, 1; Aberdeen, 1; Baltimore, 7; Beltsville*, Bladensburg, 1; Camp Meade*, Great Falls, 1; Lakeland, 1; Montgomery Co., 2; Plimmers Island, 1; Wolfsville, 1. MASSACHUSETTS: State label, 4. MICHIGAN: State label, 3. MISSOURI: State label, 4; Cedar Gap, 1; Columbia, 2*; Saint Louis, 3; Willard, Green Co.*; Williamsville, 1. NEBRASKA: Nebraska City, 6. NEW JERSEY: State label, 17; Avenel, 5; Berkeley*, Chester*, Croperill Hill, 1; Englewood*, Englewood Cliffs*, Essex Falls, 1; Fort Lee, 19*; Greenwood Lake, 1; Hillburn*, Hopatcong, 1; Houghton Hill, 2; Montclair, 1*; Moorestown*, Newark, 1; Plainfield, 1; Riverton, 1; Roselle Park*, Snake Hill, 1; South Orange, 2; Springfield*, Summit, 1. NEW YORK: State label, 6; Bear Mounts, 2; Bronx, 3*; Greenwood Lake, 2; Grymes Hill, 2; Long Beach, L. I.*; New City, 1; Orangeburg, 2; Ridgefield, 1; Staten Island, 9*; Van Cortland Park, 1; West Point, 24. NORTH CAROLINA: Julian*, Raleigh, 3; Roanoke Island*. OHIO: Sugar Grove*, Cincinnati*. OKLAHOMA: Alva Okl. Terr., 1; Blue Jacket, 6; Craig Co., 1; Latimer Co., 1; Ottawa Co., 5; Stigler, 1; Stillwater, 4; Wagoner, 1; Wilburton, 1; Wyandotte, 3. PENNSYLVANIA: State label, 4; Abington, 5; Allegheny, 1; Aspinwall, 1; Clarks Valley*, Dunbar, 1; Dauphin Co., 10; Enterline, 1; Fair Oaks, 1; Frankford, 1; Harrisburg*, 1; Hummelstown, 2*; Indiana, Monroe Co., 2; Jeannette, 25*; Linglestown, 1; Millvale, 1; Mount of Holly Springs, 1; Pittsburgh, 25*; Philadelphia, 1; Sciota, 2; Wall, 1; Wind Gap, 3; Wyomissing, 4. TENNESSEE: State label, 2; Benton Co., 2; Deer Lodge*, Lake Co., 1; Perryville, 4. TEXAS: State label, 6. VIRGINIA: Bluemont, 1; Clarendon, 1; Dyke, 1; Falls Church, 6; Glencarlyn Alex., 1; Great Falls, 3; Montgomery Co., 13; Nelson Co., 2; Pennington Gap, 1; Phoebe, 2; Suffolk, 1; Warrenton, 1. WEST VIRGINIA: State label, 1; Athens, 1; Cheat Mountains, 19; Holly Grove, 1; Kanawha Sta., 2; Pocahontas Co., 4; Ripley, 1; West Sulfur, 4.



Figs. 5-14.—Anatomical features of *Melanactes*. 5. Ventral view of male genitalia of *Melanactes piceus*. 6. Ventral view of male genitalia of *Melanactes morio*. 7. *Melanactes densus*. Dorsal (A) and ventral (B) views of male genitalia. 8. *Melanactes* sp. Male genitalia fully distended, showing everted vesicle. 9. Male antenna of *Melanactes*. 10. Hind wing of *Melanactes morio*. 11. Male antenna of *Melanactes reichei*. 12. Male antenna of *Melanactes densus*. 13. Male antenna of *Melanactes piceus*. 14. Female reproductive organs of *Melanactes* sp.

Discussion.—This is the most common and widely distributed species of *Melanactes*. It is easily recognized by its smooth and shiny appearance.

The type locality for *M. piceus* given by DeGeer is "Pensylvanie." According to the description, the type specimen is 26 mm long and 8 mm wide. It is probably in the Riksmuseum of Natural History in Stockholm.

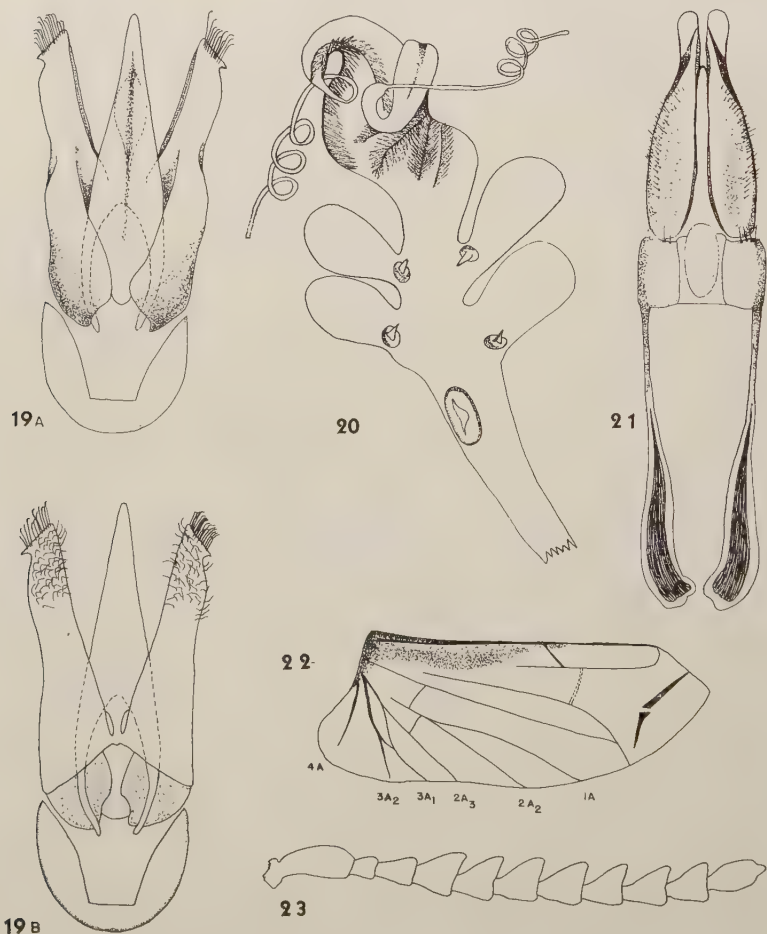


Figs. 15-18.—Female structures of *Melanactes*. 15. Female genitalia of *Melanactes piceus*. A. Dorsal view, showing the four rows of spines in the bursa copulatrix. B. Ventral view, showing also the lateral anterior row of spines. 16. *Melanactes piceus*. Eighth sternite of female and chitinous rods of the genital organs. 17. Female genitalia of *Melanactes densus*. A. Dorsal view, showing the two rows of spines in the bursa copulatrix. B. Ventral view. 18. Eighth sternite of female, *Melanactes reichiei*.

The type of *M. procerus*, in the LeConte collection at the Museum of Comparative Zoology (Type No. 2628), measures 33 mm in length and 9.5 mm in width. It agrees with the female of *M. piceus* in all characters.

Genus *Pseudomelanactes*, new genus

Description.—Large, robust. Dull black; antennae and legs reddish black. Head with front slightly depressed, rather coarsely, somewhat closely punctate; mandibles directed downward. Antennae



Figs. 19-23.—Anatomical features of *Pseudomelanactes agrypnoides*. 19. Ventral (A) and Dorsal (B) views of male genitalia. 20. Female internal genitalia. 21. Female external genitalia, with chitinous rods. 22. Hind wing. 23. Male antenna.

(Fig. 23) longer than two-thirds of the length of pronotum but not reaching hind angles; second segment small, slightly longer than wide; third, one and a half times as long as second, apically dilated; fourth to tenth broadly serrate; fourth slightly wider than long; following segments gradually narrower; eleventh elongate, constricted before apex. Pronotum from apices of hind angles to apex longer than wide, but appearing more or less quadrate; sides rather broadly arcuate at hind angles, narrowing toward apex; hind angles prominent, distinctly divergent, blunt at apex, carinate; carinae long and close to margin; marginal groove extending but slightly beyond middle, at that point fusing with margin; disc convex, rather coarsely, moderately densely punctate in front, and at the sides; punctures less well-impressed and more separate at middle and behind; sulcus absent; a prominent prescutellar tubercle present. Scutellum subquadrate, with margins well elevated and disc sparsely and finely punctate. Elytra almost twice as long as wide; sides slightly arcuate and gradually narrowed from basal third to apex; disc convex; striae well impressed at base, elsewhere indicated only by a series of fine, moderately closely-placed punctures, which gradually become deeper and more conspicuous from the center to the sides; interstriae flat except at base, rugulose and very finely punctate; humeri rounded and prominent; ninth interstria of each elytron very prominent in front and with a deep groove between it and margin. Anal cell not present in hind wing (Fig. 22). Prosternum coarsely, not closely punctured. Prosternal spine elongate, rod-like, more or less cylindrical, with a pointed tip. Propisterna more finely and closely punctate than rest of venter. Mesosternum with the sides of the mesosternal groove slightly raised, expanded laterally into two concave plates; margin of mesosternal groove more or less parallel. Epipleura provided with yellow hair at the level of the mesepimera, becoming very sparsely clothed behind it. Metasternum coarsely not closely punctate, very finely punctate at middle. Hind coxal plates narrowing gradually toward metepisterna. Tarsi on the under side clothed with a brush of golden hairs; first segment twice as long as second; other segments gradually shorter; fifth as long as first. Tarsal claws simple. Abdomen uniformly and shallowly punctate.

Male genitalia (Fig. 19) with basal piece rounded; ventral side and tip of the parameres provided with a dense clothing of hairs, curved at the tip.

Female genitalia (Fig. 20) and eighth abdominal sternite (Fig. 21) large, heavily sclerotized; distal part of vagina having a plate-like tubercle; bursa copulatrix membranous, bearing four smaller sharp pointed tubercles located at the base of the four colleterial glands; from this point the bursa becomes more sclerotized and splits into two ducts; one duct (leading to the spermatheca) has two rows of spines running for its length; the other (leading to an accessory gland) is provided basally with a V-shaped row of spines, flanked by an additional row on each side.

Discussion.—The relationships of this genus are discussed below. It contains only a single species, *Melanactes agrypnoides* Van Dyke, which automatically becomes its type species.

***Pseudomelanactes agrypnoides* (Van Dyke) new combination**

Melanactes agrypnoides Van Dyke (1932, p. 446).

Description.—Male. Length 26.5 to 28 mm; width 8 to 9 mm. Large, black, not very shiny beetles. Antennae heavy, not reaching hind angles of pronotum; first three segments scarcely pubescent; remaining segments densely covered with short yellowish hairs (visible only under high magnification). Pronotum with disc more shiny than elytra, entire surface covered with small setae (visible only under high magnification). Epipleura provided with abundant yellowish hair at the level of the mesepimeron, becoming sparsely clothed toward the metasternum. Genitalia as in Figure 19.

Female. Length 31 mm; width 9.5 mm. Genitalia as in Figure 20.

Distribution.—This species occurs only in the southern part of Arizona. It has been collected from July 10 to September 29. Only seven specimens have been collected of this rare species.

ARIZONA: Gila River at Gerónimo, 2600 ft., Graham Co., August 6, 1948, willow-mesquite-cotton area, W. Nutting and F. Werner, CNHM, 1; Nogales, August 14, 1906, F. W. Nunenmacher, CAsC., 1; Santa Rita Mountains, September 29, 1922, Werner collection, 1; July 24, W. J. Chamberlin, Lane collection, 1; Tucson, 2300-2500 ft., July 13, 1915, Wickham collection, USNM, 1; Wickenburg, Maricopa Co., July 10, 1953, Etta Beer, Lane collection, 1; (Mr. Lane informs me that there is another specimen with the same data in the Beer collection).

Discussion.—Only a single female was available for study. This specimen is larger than any of the males and has the last visible sternite less acute. Otherwise, it is externally like them.

The species was originally described from a single specimen from Nogales, Arizona. This specimen, a male, is in the collection of the California Academy of Sciences (type No. 3193).

PHYLOGENY

Relationships of the Genera *Melanactes* and *Pseudomelanactes*

Although the genera *Melanactes* and *Pseudomelanactes* are both members of the subfamily Pyrophorinae, their relationship to each other is not a particularly close one. *Melanactes* belongs to the tribe Denticollini (=Lepturoidini). *Pseudomelanactes*, on the other hand, is herein assigned to the tribe Pyrophorini.

There are a great number of characters found in adult *Melanactes* beetles that occur also in other members of the tribe Denticollini. The mandibles are typically directed forward. The scutellum is heart-shaped. As in most Denticollini, the mesosternum is reduced to some extent and is not extended to form plates as in the Pyrophorini. The hind wings are like those of other genera of the Denticollini studied (*Ctenicera* Latreille, *Denticollis* Fabricius, and *Elatichrosis*

Hyslop²) in having a crossvein between veins $2A_3$ and $3A_1$, forming the so-called anal (or wedge) cell (Fig. 10). The basal piece of the male genitalia is more or less quadrate in *Melanactes*, as in *Ctenicera* and *Denticollis*. In *Elatichrosis* the basal piece is rounded, as in the Pyrophorini.

The prosternal spine in *Melanactes* is peculiar in that it is wide, very deep, and wedge-shaped. This particular form of spine is found in only one other elaterid available to me for study. This is the Australian *Elatichrosis illita* (Cand.), a single representative of which was received on loan from the personal collection of Mr. Lane.

The characters of the genus *Pseudomelanactes* are most similar to those of the members of the tribe Pyrophorini. The mandibles are directed downward. The scutellum is subquadrate and has elevated margins. The prosternal spine is a long, rodlike process very much like that found in the pyrophorines *Lanelater* Arnett and *Pyrophorus* Illiger. The mesosternum is expanded into concave plates, as it is in the other Pyrophorini studied. The crossvein which closes the anal cell in the Denticollini is not present in any members of the tribe (Fig. 22). As mentioned above, the basal piece of the male genitalia is rounded. Finally, a prescutellar tubercle is found on the pronotum in *Pseudomelanactes* as well as in *Lanelater* and *Pyrophorus*. *Lanelater* is more specialized than *Pseudomelanactes* in having a prosternal groove, while *Pyrophorus* is more specialized in possessing light-producing organs.

The nearest relative of *Pseudomelanactes* that I have seen during my study is an elaterid represented by a single specimen in the Chicago Natural History Museum labeled Tefe (Upper Amazon River), Brazil. This species has all of the characters of *Pseudomelanactes* discussed above and, in addition, is very similar to the genus in the general form of the body and the shape of the pronotum. Unfortunately, I have not been able to identify the specimen.

While I believe that *Melanactes* and *Pseudomelanactes* may be satisfactorily placed in the tribes Denticollini and Pyrophorini, respectively, their phylogenetic relationships to the other members of their tribes remain rather obscure. As intimated in the preceding discussion, *Melanactes* is possibly more closely related to the Australian genus *Elatichrosis* than to *Ctenicera* or *Denticollis*, and there is evidence suggesting that *Pseudomelanactes* is of neotropical origin. Much additional study of both tribes is needed to elucidate the relationships of the genera within them.

Phylogeny of the Species of *Melanactes*

Because of the incompleteness of the fossil record, it is necessary to rely largely on comparative morphology of living species in reconstructing the evolutionary history of the genus. The tribe Denti-

² Although the genus *Elatichrosis* has never been formally included in the tribe Denticollini, there seems to be no reason why it should not be.

collini first appears in the fossil record in the Lower Oligocene, where it is represented by the extant genera *Athous* Eschscholtz, *Limonius* Eschscholtz, and *Cryptohypnus* Lacordaire. In the Miocene there are some elaterid fossils that have been assigned to the genus *Ctenicera* Latreille as well as a specimen from Florissant shales described by Wickham (1908) as *Melanactes cockerelli*. This last fossil seems to have all the external morphological characters of the genus *Melanactes* except that there is some uncertainty as to whether it has the hind angles of the pronotum carinate. If it is not a true *Melanactes*, then it is apparently a very close relative of the genus. Among the living species of *Melanactes* it most closely resembles *M. densus*.

The modern species of *Melanactes* are, in general, very similar to one another morphologically, and it is therefore difficult to find a variety of characters from which to deduce phylogenetic relationships. The most satisfactory arrangement seems to be the one shown in Figure 24. The following discussion is an explanation of the line of reasoning followed in arriving at this arrangement.

In attempting to group the species of *Melanactes* phylogenetically, it is immediately apparent that the two most similar species are *M. puncticollis* and *M. consors*. These two species differ only in the degree of convexity of the pronotum and elytral interstriae. According to the present records, they are strictly allopatric in distribution.

Melanactes piceus shows a close relationship to *M. puncticollis* and *M. consors* in sharing with them the presence of four median rows of spines in the bursa copulatrix of the female genitalia (Fig.

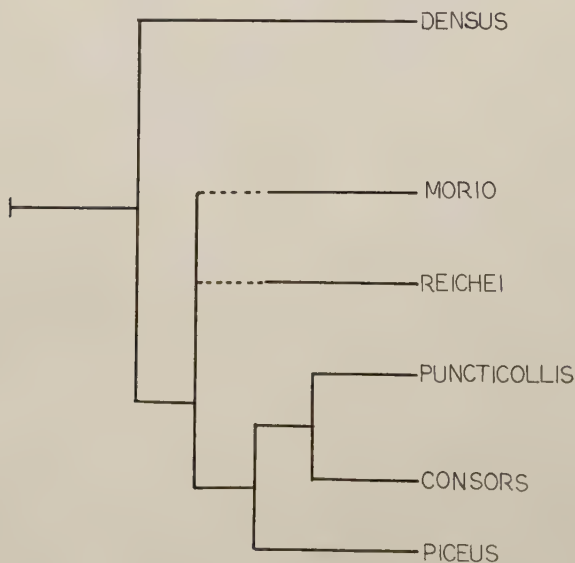


Fig. 24.—Phylogenetic tree of the species of *Melanactes*.

15). It differs from them in that the elytra interstriae are flat and shiny and the striae are shallowly punctate. These elytral characters were probably present in the earliest ancestor of the genus.

The species *M. morio* and *M. reichei* have an obscure origin. They are associated in the tree shown in Figure 24 on the basis of their having only two rows of spines in the bursa copulatrix. Each species has a number of characters which are probably specialized. For instance, in *M. reichei* the body is elongate and there are small appressed setae on the pronotum. In the case of *M. morio*, a great convexity of the interstriae is found and the striae are provided with deep punctures.

Melanactes densus is geographically and morphologically the most distinct species of the genus. It is characterized by a general lack of hair, by flat, canaliculate interstriae, and by the presence of two rows of spines in the bursa copulatrix (Fig. 17). All these characters appear to be primitive for the genus.

It is supposed that *M. densus* evolved from an ancestral population that was at one time widely distributed in the United States and that for some reason was subsequently divided into a western and eastern segment. The western segment of the population gave rise to *M. densus*, which is now confined to the West Coast. The eastern segment produced the remainder of the species of the genus.

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The Lens as an Indicator of Age in the Raccoon

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ABSTRACT: The growth rate of the lens of the eye was studied as a means of determining age in the raccoon. One hundred and nineteen raccoons were studied, including 3 embryos, 18 born in captivity, 42 captured in the wild and kept in captivity for varying periods, and 56 wild animals. Ages of all but those born in captivity were estimated, but these estimates are believed to have an error of no more than ± 2 months. Weights of the dried lenses were used to construct a growth curve which will indicate the month of birth for animals less than 12 months of age, and will estimate the relative age composition of groups of older animals.

There are several useful techniques for determining the ages of dead and live raccoons (*Procyon lotor*) from birth through approximately 8 months of age and for separating males and females less than 1 year of age from those of more than 1 year during the hunting and trapping season (Sanderson 1950 and unpublished). No reliable technique is available for further segregation of raccoons by age after they have passed their first year of life. Lord's (1959) work on the growth rate of the lens of the cottontail rabbit (*Sylvilagus floridanus*) prompted this study of age-defining capacity of the lens in the raccoon.

Acknowledgments.—This is a contribution from Illinois Federal Aid Project No. 56-R, the Illinois Department of Conservation, the United States Bureau of Sport Fisheries and Wildlife, and the Illinois Natural History Survey, co-operating.

Drs. T. G. Scott, C. O. Mohr, and R. E. Yeatter and Barbara A. Chipman read the manuscript and made helpful suggestions. Special thanks are due to Conservation Officers Conrad Foley and Loyd Skinner and to B. J. Verts who supplied many of the raccoons used in this study and to Dr. R. D. Lord, Jr., for helpful suggestions.

METHODS

Raccoons, some born in captivity and others captured in the wild, were kept in captivity varying lengths of time to provide material for this study. Lenses were also obtained from wild raccoons which were live-trapped, ear-tagged, released, and recovered later. Young, unmarked, wild animals were also studied. Ages of all young except those born in captivity were estimated on the basis of a growth curve drawn by using body weights of nursing young born in captivity for the early part of the curve. Later points on the curve were established by plotting weight changes of live-trapped young at subsequent recaptures. The error in these estimates is believed to be no more than ± 2 months (Sanderson, unpublished).

Three males and two females were castrated in order to study possible effects of lack of sex hormones on the growth rate of the lens.

Eyes were removed from a raccoon which was killed a few minutes after birth and from three embryos which were aged by interpretation of data from Llewellyn (1953). The eyes of the raccoons were preserved in 10 per cent formalin. After hardening for several days the lenses were removed, dried in an oven, and weighed to the nearest tenth of a milligram on a micro-torsion balance (see Lord, 1959, for further details of the methods used).

The right and left lenses were weighed in most cases, but there were no significant differences. The dry weight of one lens from each raccoon was plotted to construct a growth-rate curve; however, if the weights of both lenses were available they were averaged, and the average weight was used. Other measurements of the lens were not taken because Lord (1959) found that dry weight gave the best curve in cottontails.

RESULTS

The data (Table I) indicate good correlation between the dry weight of the lens and age up to 12 months (Fig. 1). There is considerable variation as the curve bends between 12 and 20 months of age; after 20 months the curve ascends very slowly.

Initially, males and females were considered separately, but no differences were apparent according to sex. Also, the data were plotted separately for captive and wild animals, but no consistent differences could be seen between 63 captives, including 3 embryos, and 56 wild animals which were studied. There were too few captive and wild raccoons to construct a growth curve of the lens from one group. All but 21 of the captive animals were captured in the wild and were held in captivity for varying lengths of time. Possibly

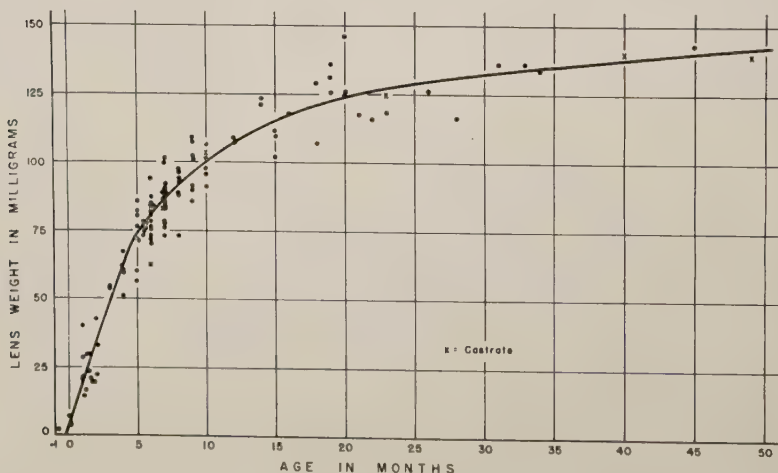


Fig. 1.—The growth-rate curve of the lens based on 119 raccoons of known age.

TABLE I.—The dry weights of lens of raccoons of known ages and estimated ages¹

Age (Days)	Wgt. (mg)	Age (Days)	Wgt. (mg)	Age (Months)	Wgt. (mg)
-21	2.2	180	62.8	9	85.4
- 1	1.8	180	70.1	9	89.4
- 1	2.6	180	71.7	9	92.0
E 0	6.2	180	72.8	9	101.8
E 29	20.2	180	75.4	9	102.2
30	28.7	180	75.6	9	107.6
30	40.0	180	78.1	9	109.3
E 34	14.0	180	80.5	10	91.2
E 34	21.6	180	81.4	10	95.2
E 38	16.7	180	82.4	10	97.3
40	29.0	180	83.8	10	101.6
E 46	23.2	180	83.9	10 ²	102.4
E 49	20.8	180	84.0	10	106.4
49	29.2	180	87.5	12	106.4
E 51	18.5	180	94.3	12	108.4
E 52	19.8	E 206 ²	83.4	14	121.2
60	42.6			14	122.7
E 62	22.3	*		15	102.0
E 65	33.7			15	109.6
90	54.2	7	73.0	15	111.4
90	54.3	7	76.0	16	117.6
120	51.4	7	77.3	18	106.4
120	59.0	7	77.4	18	129.2
120	60.5	7	78.4	19	125.7
120	63.8	7	78.8	19	130.8
120	67.0	7	80.5	19	135.7
150	56.6	7	81.4	20	124.8
150	60.1	7	81.8	20	125.4
150	71.6	7	83.6	20	145.6
150	76.8	7	83.8	21	117.2
150	80.1	7	84.5	22	125.4
150	82.4	7	84.9	23	118.2
150	85.6	7	92.2	23 ²	124.6
E 154	71.9	7	99.8	26	126.2
E 167	68.4	7	101.2	28	116.0
E 168	78.5	8	73.3	31	135.6
E 169	74.0	8	88.4	33	135.6
E 172	75.6	8	88.8	34	133.0
E 172	77.7	8	92.4	40 ²	139.5
		8	94.4	45	142.8
		8	96.5	49 ²	138.4
		8	96.9		

¹ E = exact age, all others are estimated ages. Estimated ages have no more than a $\pm$ 2-month error.

² Castrate.

* (Months).

this fact increased the variability of the data because Lord (personal communication) has found that lenses in wild cottontails grow at a slower rate than they do in captives. Probably contributing to the variance, especially prior to 12 months of age, is the fact that ages were estimated for all of the wild and all but 21 of the captive raccoons. There may be as much as a ± 2 -month error in estimates of the age of raccoons born in the wild. Because lens weights showed considerable variation, especially after 12 months of age, attempts were made to relate body weight and length to lens weight; however, these data gave no better curves than did a direct plot of the lens weights.

Three males and two females were castrated. One male, castrated when 109 days of age, died at 206 days of age. A second male, castrated when approximately 9 months of age, died 14 months later. The third male, castrated prior to 6 months of age, died when 10 months of age. One female, castrated when approximately 26 months of age, died at 49 months of age. The second female, castrated at 17 months of age, died 23 months later. The weights of all their lenses were typical of those of intact animals (Fig. 1).

DISCUSSION

The lens indicates the month of birth for individual raccoons up to approximately 12 months of age. While it may be used to determine the relative age composition of groups over 12 months of age, because of individual variation, it cannot be used to determine the specific age of the animals in the group.

The lens-growth curve of the raccoon is similar to those of the cottontail (Lord, 1959) and the gray fox (*Urocyon cinereoargenteus*) (Lord, in press), except for one important difference. In all three species the data show but little spread up to where the curve bends most abruptly, but then the variation increases and finally decreases again. The ages at which the curves bend seem to occur in all three species at about the time they reach the adult size and, in the raccoon, the bend in the curve corresponds roughly with the time over which the animals reach sexual maturity. Because the raccoon curve is much flatter after this point than that of either the cottontail or the gray fox, it is not possible, from the present data, to determine the year of birth after the first year.

Practically all raccoons in Illinois are 4 to 10, 16 to 22, 28 to 34, etc., months of age during the hunting and trapping season in Illinois, and most fall into the narrower age groups of 6 to 8, 18 to 20, etc., months (Sanderson, unpublished). This fact will reduce the amount of overlap to be found between year classes if this technique is used to analyze the age composition of animals harvested during the open season.

Because there are fewer animals in each succeeding older age group than there are in the younger groups, there are fewer animals

28 to 34 months of age with lenses falling into the 16- to 22-month age group than there are animals 16 to 22 months of age with lenses falling into the 28- to 34-month age group. Thus, individual variation will tend to skew the age composition in favor of the older age groups.

Although only five castrate animals were studied, the fact that the weights of their lenses fall within the groups for intact animals of similar ages indicates that age at attainment of sexual maturity may have little effect on growth rate of the lens.

Other techniques such as those involving the baculum (Sanderson, 1950) and epiphyseal closure (Sanderson, unpublished) are easier and more convenient to use for separating a population into two age groups: those less than 1 year of age and those older than 1 year of age. Epiphyseal closure can also be used in live animals by use of X-rays. However, the lens seems to offer possibilities for separating a population into more than two age groups and for determining the month of birth for raccoons less than 1 year old.

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Notes on the Local Distribution of *Peromyscus leucopus* and *Zapus hudsonius*

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ABSTRACT: The factors influencing the local distribution of *Peromyscus leucopus* and *Zapus hudsonius* were studied in seven habitats (old field, hardwood swamp, coniferous swamp, bog mat, spruce burn, upland hardwood, and grass sedge marsh) in southern Michigan. The environmental factors considered were vegetation type, cover (fallen trees, brush, leaf litter), temperature, food, moisture, and interspecific competition. *P. leucopus* permanently inhabited only wooded habitats (those with trees or shrubs). There was no indication of an avoidance of herbaceous vegetation; there appeared to be a positive response to a tree-shrub type of vegetation. The reason for such a response was not determined. Among the forested areas, an oak-hickory upland was the most favorable habitat. A larger and more stable food supply (acorns and nuts) appeared to be the major factor responsible for the greater abundance of *P. leucopus* in this habitat. Temperature, moisture, cover, and interspecific competition were not important factors in the selection or avoidance of a particular habitat. *Z. hudsonius* was found only in moist situations and was slightly more abundant where there was standing water. Vegetation, temperature, cover, and interspecific competition were not important factors in its local distribution.

During the course of a field study of the local distribution of microtine rodents and shrews in southern Michigan, data were obtained pertaining to the white-footed mouse, *Peromyscus leucopus*, and the jumping mouse, *Zapus hudsonius*. Although the study was not designed primarily for these two species, there was sufficient variation in the habitats to determine the influences of certain factors. Since information concerning the local distribution of small mammals is relatively rare in the literature, it seems advisable to make these data available.

The information presented in this paper has been extracted from a thesis presented in partial fulfillment of the degree of Doctor of Philosophy in the University of Michigan.

DESCRIPTION OF THE STUDY AREA AND METHODS

Study area.—All the work was done in the University of Michigan's Mud Lake Research Area in southern Michigan. Seven habitats (old field, hardwood swamp, bog mat, spruce-birch-larch swamp, spruce burn, oak-hickory upland, and marsh) within the area were selected for study. In addition, six transects were established to cross as many types of habitat as possible. The study areas and transects are described in detail elsewhere (Getz, 1961a, b).

Methods.—Three methods of sampling the abundance of small mammals were utilized. (1) A rectangular study area consisting of 75 trap stations placed in a grid pattern with an interval of 12 meters

was established in all habitats except the spruce burn. This latter area was small and contained only 30 stations. Each study area was trapped for two, 3-night periods, one in October to November, 1957, and the other in January, 1958. One trap (snap-traps in all areas except the old field and marsh; these were live-trapped as described below) was placed at each station. (2) The old field (2.5 hectares) and a 4.4 hectare portion of the marsh were marked off in a grid pattern with a 12 meter interval. Each station was live-trapped for 5 nights each month, September, 1957, through September, 1958. All individuals were marked by toe clipping. (3) Six transects were subdivided into 15 "segments" according to physiognomy of the vegetation, type of substrate and its moisture content, leaf litter, and debris (logs, dead brush, and litter). A trapping station was located every 3 meters along each transect. Each station was trapped for 7 nights during the first two weeks of September, 1958. The capture data for each of the 15 segments were converted to a common factor (number of captures per 500 trap nights) for comparison.

Study of the environmental factors.—The factors studied included vegetation (type and physiognomy), cover, moisture (including standing water), temperature, and food. The methods used to study the environmental factors have been described elsewhere (Getz, *op. cit.*).

Statistical analysis.—Those data that lend themselves to statistical treatment have been analyzed by use of the Spearman rank correlation coefficient (Siegel, 1956). In the following discussions the correlation coefficient (r_s) as well as the probability or level of significance (P) from Siegel (*op. cit.*) are given with statements of correlation or no correlation.

RESULTS

Peromyscus leucopus

Vegetation.—The white-footed mouse is characteristic of forested or wooded areas (Burt, 1940; Linduska, 1950; Johnson, 1926; Wetzel, 1958; Jameson, 1949), but is sometimes found in grassy situations (Blair, 1940; Howard, 1949). Burt (*op. cit.*) believed that the individuals found in grassy areas represent young or unsettled animals. Blair (*op. cit.*) found them to be more abundant in such areas during the summer while Howard (*op. cit.*) found them to be more abundant during the winter. Burt further stated that it may avoid those areas in the forest that have a grass stratum. Linduska (*op. cit.*) also gave evidence to support the avoidance of grassy sites within the wooded areas.

In the present study, *P. leucopus* was limited primarily to areas containing trees or shrubs (Table I; Figs. 1 to 5). (Note. The transect data from the oak-hickory are probably biased. Almost all resident animals were removed when the area was trapped in November, 1957, and January, 1958. Since this area is ecologically isolated from other forested situations, it is possible that the population had not recovered by the time of the transect trapping.) The small number

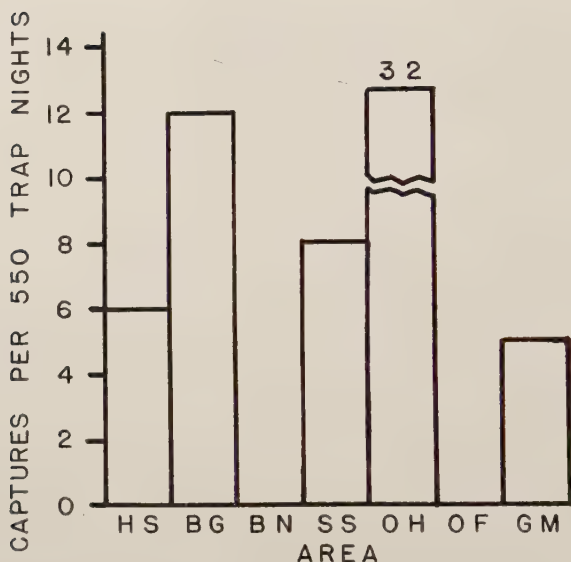


Fig. 1.—Relative abundance of *Peromyscus leucopus* in seven habitats. Fall and winter trapping data combined. HS, hardwood swamp; BG, bog mat; BN, spruce burn; SS, spruce-birch-larch swamp; OH, oak-hickory upland; OF, old field; GM, grass-sedge marsh.

captured in herbaceous vegetation as well as on the bog mat can in most cases be attributed to animals moving from one woody area to another or to the foraging of the individuals for short distances into nearby non-forested areas. However, those individuals occurring in the marsh during the winter (Table I) were not “wandering”, but became established for at least two to three months; also they all were adult individuals. Although the area in which they occurred was small, there was an indication that home ranges were established. During the remainder of the year, the individuals captured in the marsh were obviously only moving through the area.



Fig. 2.—Symbols used in the structural diagrams in Figs. 3 and 4. Modified from Dansereau, 1957.

The vegetation of one portion of the marsh (0.8 hectares) consisted primarily of *Potentilla fruticosa*. This species, while having a physiognomy similar to that of a low (0.5 meter) forb, is woody. This area was not inhabited by *P. leucopus*.

That trees are not necessary for the presence of *P. leucopus* was

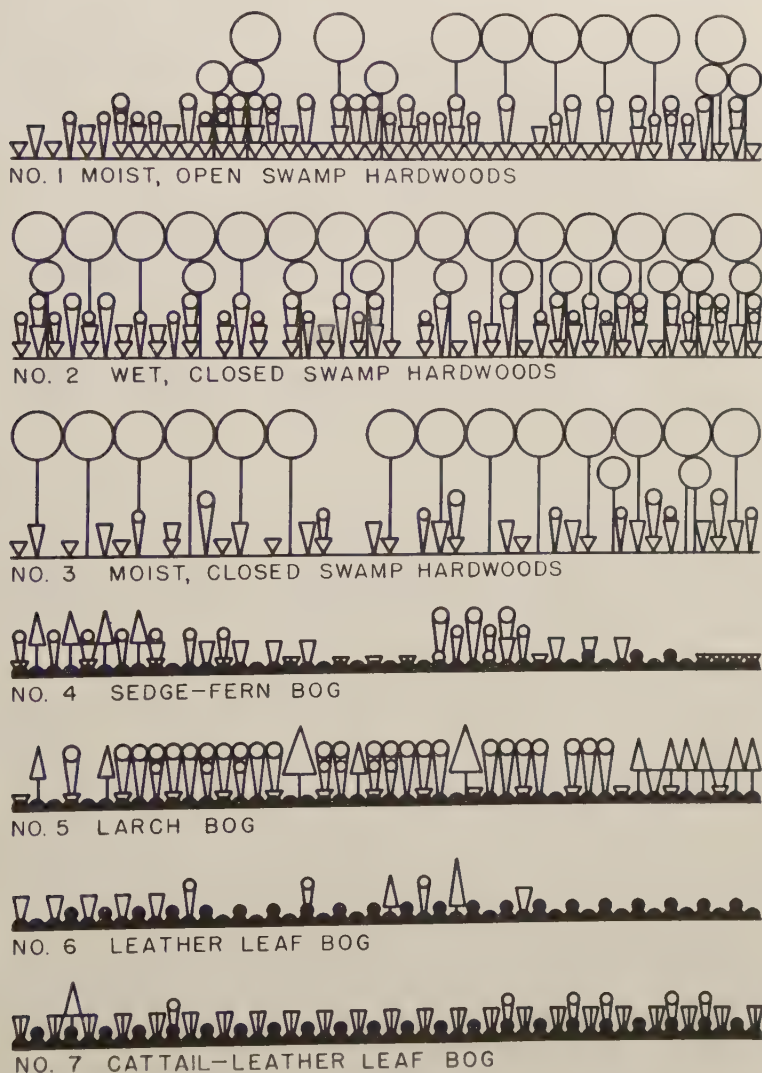


Fig. 3—Structural diagrams of the vegetation from transect segments No. 1 to 7.
See Fig. 2.

indicated in the *Cornus-Populus* stand in the marsh. This stand consisted of a dense stand of *Cornus racemosa* (2.5 to 3 meters tall) and a few small *Populus tremuloides* (5 to 6 meters tall). At least one or two individuals were present in this site throughout the year (some

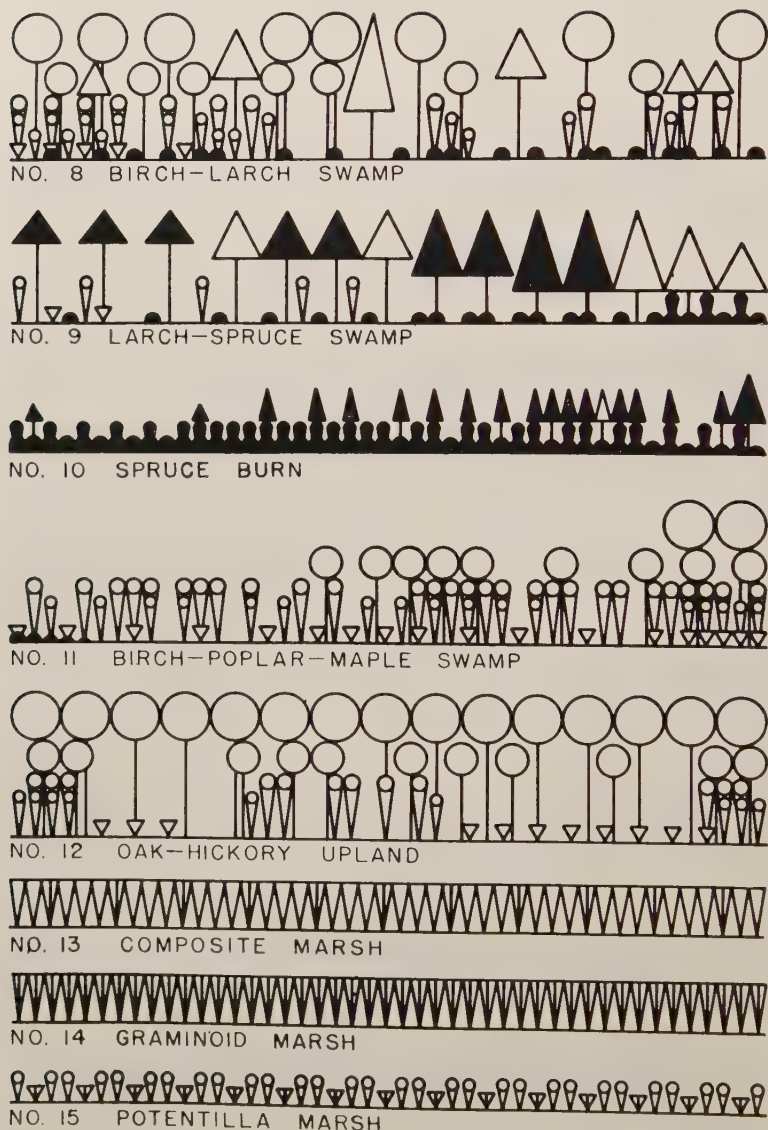


Fig. 4.—Structural diagrams of the vegetation for transect segments No. 8 to 15.

were present in the area for several months so "wanderers" alone were not involved).

Presence of a field or shrub stratum in a wooded area had no apparent influence upon the local distribution of *P. leucopus* as it was abundant in areas where they were present as well as those without such strata (Fig. 5). During the September, 1957, trapping period, 12 live-traps were set in an old pasture adjoining the old field. The traps were in an area in which the vegetation consisted of scattered oak and hickory trees and *Poa pratensis*. Three *P. leucopus* were captured in 5 days of trapping. The nest of a pair of white-footed mice was found under some debris in this site in May, 1958. Observations of acorns and nuts that had been eaten by mice during the period of the study indicated at least a few *P. leucopus* to be present during most of the year.

Cover.—Brand (1952) found that *P. leucopus* is most abundant in areas (within an oak-hickory stand) in which much cover in the form of a shrub stratum or fallen trees and debris is present. In the present study there was no correlation between the amount of cover (in the form of logs, brush, and other debris) in the various habitats

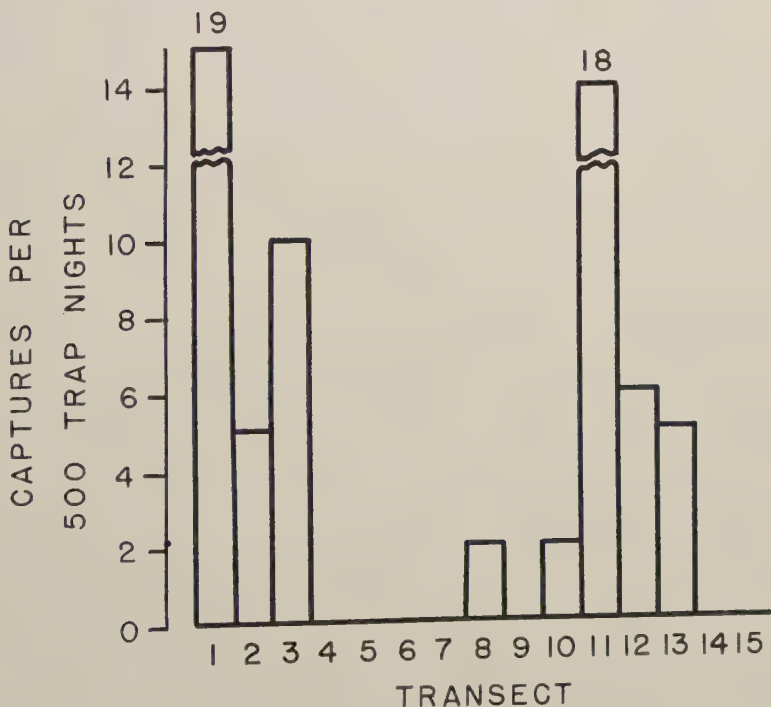


Fig. 5.—Transect captures of *Peromyscus leucopus*. Captures in No. 12 biased (see text).

and the abundance of *P. leucopus* (r_s , .07; P , .05 = .714). Cover of this type was, therefore, not the major factor in the selection of a particular habitat.

Moisture.—Both upland hardwoods and swamp hardwoods have been listed as favorable habitats. Layne (1958) found *P. leucopus* to be particularly abundant in low, swampy woodlands in southern Illinois. Enders (1930) stated that it was able to accommodate to a greater range of moisture conditions than any other rodent. Nicholson (1941) found that few individuals lived on the ground during the summer; they were living and nesting primarily in the trees. This would tend to reduce the influence of excessive moisture or standing water upon the local distribution of *P. leucopus*.

McCarley (1954) found, in Texas, that when *P. leucopus* occurred alone it was present both in uplands and lowlands. When sympatric with *P. gossypinus* (a closely related species), it was found only in the uplands. This may indicate that the upland hardwoods are more favorable for *P. leucopus* while the lowlands are marginal habitats. The reasons for such a distribution were not indicated, however.

A definite negative response to excessive moisture was not noticed in the present study. They were less abundant in the swampy areas, but this may in part be a response to a lesser available food supply (see below). Transect segment No. 2 in the hardwood swamp, which was lowest and contained water during the spring and early summer, had fewer captures than the other two, slightly drier, segments of the hardwood swamp (Nos. 1 and 3). Likewise, those individuals captured during the grid trapping of the hardwood swamp were taken from the higher portion. The wetter segment of the transect was located in a narrow portion of the hardwood swamp (about 50 meters wide, Getz, 1959a); it, therefore, drew its animals from a

TABLE I.—*Peromyscus leucopus* captures in a grass-sedge marsh (1290 trap-nights each month); September, 1957 to September, 1958

Month	No. captures	Average capture per individual
September	2	1.0
October	12	1.3
November	21	1.3
December	17	1.1
January	47	3.0
February	25	2.5
March	13	2.1
April	1	1.0
May	1	2.0
June	0	
July	3	1.5
August	3	1.5
September	13	1.3

smaller area. This quite possibly biased the data and gave the impression of few numbers present in such a situation. Because of this and owing to the tendency of *P. leucopus* to be somewhat arboreal, I do not believe excessive moisture to be the primary factor in their avoidance of the wet areas.

Food.—Food of *P. leucopus* consists primarily of seeds, nuts, and acorns (Cogshall, 1928). Fleshy fruits are utilized in season. Insects and other invertebrates have been recorded, but do not appear to form a major part of their diet. Cogshall (*op. cit.*) concluded that food is probably not an important factor in limiting the local distribution of *P. leucopus*. She referred to the species of food plants present and not to the abundance of food in any particular area. Lindeborg (1941) speculated that food availability may influence fluctuations in population densities of *P. leucopus*. Bendell (1959) gives data that show food to be an important factor in regulating population sizes of the white-footed mouse.

In the present study food appeared to be an important factor in the local distribution of *P. leucopus*. This species was scarce in those areas having a lesser stable year-round food supply. From the lists of the more abundant plant species of each area (Getz, 1961a, b), the oak-hickory is most favorable in regards to having a year-round food supply. While species such as *Acer rubrum*, *Vaccinium corymbosum*, *Maianthemum canadense*, and *Rubus pubescens* (which occurred in the swampy areas) may yield an abundant supply of food at certain seasons, their seeds are not as available for later use as are the acorns and nuts of oaks and hickories. These latter trees are most abundant in the upland areas. The presence of such a food supply probably is a major factor enhancing the numbers of white-footed mice in the drier areas while limiting the numbers in the moist and wet areas. Acorns and nuts are utilized the year round as shown by the freshly eaten remains of such items in the oak-hickory at all times of the year.

The spruce-birch-larch area, and especially the spruce portion, which was particularly low in available food, was almost entirely avoided (Figs. 1 and 5). Fallen trees, debris, and shrubs appeared to be as abundant as in other areas that were utilized. Transect segment No. 8 (in the birch-larch stand) was somewhat higher and drier than segments Nos. 1 and 3 of the hardwood swamp. *P. leucopus* captures were much higher in the latter segments, however (Fig. 5). A less available food supply during the fall, winter, and spring seems to be a most likely reason for such results. Similarly the number of captures from segment No. 1 of the hardwood swamp, in which there were a few oak trees (*Quercus macrocarpus*), were higher than from segment No. 3 in which oak trees were absent. This, too, may be a response to a greater food supply in segment No. 1, although the amount of cover is also greater in No. 1 than in No. 3 (Getz, 1961a). Both factors may, therefore, be operating to increase the number of white-footed mice in segment No. 1.

Temperature.—Dice (1922) showed that, under experimental conditions, *P. leucopus* was able to live at a temperature of 0°C in a saturated air with no noticeable ill effects. Sealander (1952) found that *P. leucopus* could tolerate temperatures from $+35$ to -25°C . It was also found by Sealander (1951) that this species may become acclimatized to lower temperatures in the winter and to higher temperatures in the summer. He further concluded (1953) that behavioral responses (burrowing, huddling, and nest building) may allow the animals to survive the effects of air temperatures below those to which they are acclimatized. Such reactions as these would tend to diminish the effects of temperature upon local distribution. Hatfield (1938) found *P. leucopus* to be less active on cold nights. This indicates a behavioral response resulting in the avoidance of excessively low temperatures.

Temperatures had no obvious influence upon the local distribution of *P. leucopus* in the present study. Temperature data obtained in the various areas (Getz, 1961a, b) show that extremes beyond those tolerated by *P. leucopus* did not occur in most habitats. In other areas such extremely low temperatures were of so brief a duration that the animals could survive by seeking shelter in their nests. The white-footed mouse could therefore, tolerate or avoid the low extremes encountered in the various types of situations. That low temperature did not greatly affect *P. leucopus* was indicated by observations obtained from examining tracks in the snow after one of the coldest nights of the year (4 January 1958, which had a surface temperature low of -20°C). A light snow had fallen the evening before and all tracks observed were made during that night. *P. leucopus* had been quite active as had other species of small mammals. If not affected to the extent of being inactive at this low temperature, it seems doubtful that low temperatures could influence their local distribution. The variations in the low temperatures in the hardwood swamp, spruce-birch-larch swamp, and the oak-hickory upland were not great enough to be deemed an important factor in the presence or absence of *P. leucopus* in these habitats.

Since the white-footed mouse is almost entirely nocturnal in habits (Johnson, 1926; Behney, 1936; Getz, 1959b), it is not normally exposed to the higher temperatures. High temperatures are, therefore, probably not a major factor in its local distribution.

Interspecific competition.—Nothing was observed to indicate that other species had an influence upon the distribution of *P. leucopus*. As discussed above, several white-footed mice moved into the marsh during the winter. This site also supported as high a population density of *Microtus pennsylvanicus* as any other portion of the marsh (Getz, 1961b). The two species occurred together for several months with no noticeable effects. Evidently no serious competition occurred.

Conclusions.—*P. leucopus* occurs in wooded areas and does not permanently inhabit those predominantly herbaceous. Under certain circumstances, however, they are found in the latter types. This is

especially true of those individuals moving from one wooded area to another or of those unsettled animals in search of a suitable habitat. There may also be some movement from the wooded areas into nearby grassy areas during the winter. The reasons for such a movement have not been explained.

Within a forested area (other factors being suitable) *P. leucopus* tends to inhabit those sites which contain more fallen trees, dead stumps, and other debris. Likewise, the presence of a shrub stratum also results in higher population densities. The presence of logs, debris, and shrub strata does not influence the selection or avoidance of a particular type of wooded habitat, however. In the present study some areas with many fallen trees and other debris were avoided while others with relatively less cover had high population densities of *P. leucopus*. Those areas with a field stratum of grass-like vegetation may be avoided, but a stratum composed of forbs is not avoided. Likewise, during the winter several individuals lived in a grass-sedge marsh for several months.

The present study revealed no explanation for the occurrence of *P. leucopus* primarily in woody vegetation. An avoidance of a particular type of vegetation as in the case of *Microtus pennsylvanicus* (Getz, 1961b) does not appear to be a factor with *P. leucopus*. Rather, it would appear that there is some positive response to a woody type of vegetation. Food does not appear to be such a factor in their apparent preference for wooded areas as the seeds from many of the forbs in herbaceous areas are readily utilized and are capable of being stored. The individuals that moved into the marsh during the winter utilized the seeds of the forbs that grew in this habitat. Wetzel (1958) believed the preference for habitats with trees is "psychological" in nature or a result of a well-developed climbing ability. The occurrence of the white-footed mouse primarily in wooded areas may in part be explained by its well-developed ability to climb (Horner, 1954). In the present study it did not occur in an area in which the vegetation, while woody in nature, had a physiognomy similar to that of forbs rather than one of trees or shrubs. This tends to support the statement concerning climbing ability. Nicholson (1941) found that *P. leucopus* nested primarily in trees. Whether this is merely a result of the utilization of the type of nest sites available in the forested habitats or an indication of preference for areas having such nest sites has not been demonstrated.

There were higher densities in the drier areas in comparison with those that were wet (i.e., swamps). Although determination of the primary factor involved was not possible, moisture alone does not appear to be the major cause of avoidance of wet areas. Those low areas not having trees such as oaks, hickories, or other nut producers, would not be apt to have a year-round food supply. It appears from consideration of the data obtained in this study that the amount of food available was the more important factor. Excessive moisture may be a contributing factor, however.

As stated above, the amount of available food is an important factor in the local distribution of *P. leucopus*. Those areas that furnish a year-round food supply are able to support higher population densities than are those in which the food supply is abundant, but seasonal.

Surface temperature lows in this study did not vary greatly in the forested areas. Although rather low temperatures did occur at times, seldom did they exceed those that *P. leucopus* is capable of tolerating. Owing to the acclimatization of *P. leucopus* to low temperatures in winter, this factor probably is not important in its local distribution. Should excessively low temperatures occur for short periods of time, behavioral responses such as retreating to nests, huddling, shivering, etc. are sufficient heat conserving mechanisms to allow the animals to survive. The nocturnal activity pattern of the white-footed mouse keeps it from being exposed to high temperatures. High temperature, therefore, is not an important factor in the local distribution of this species.

No influence upon the local distribution of *P. leucopus* by other species was noted in the present study. In regions in which more closely related species also occur competition may result in its being restricted to certain situations (e.g., upland hardwoods).

Zapus hudsonius

The jumping mouse occurs primarily in moist areas (Burt, 1948; Gunderson, 1950; Sheldon, 1938; Goodwin, 1932; Quimby, 1951). Goodwin (*op. cit.*) also found it in dry areas some distance from water. The above papers do not indicate that *Z. hudsonius* is restricted to any particular type of vegetation. It has been recorded from all types ranging from upland hardwoods to bogs and grassy areas. *Z. hudsonius* hibernates during the winter months and thus is not subjected to extremely low temperatures.

Although only a small amount of data was obtained concerning the jumping mouse, a few general conclusions can be made in regard to its local distribution.

Vegetation.—The type of vegetation did not influence the local distribution of *Z. hudsonius*. It was captured in all major types of vegetation except the spruce-birch-larch swamp and oak-hickory upland (Fig. 6). Numerous individuals were captured in the marsh in live-trap stations immediately adjoining the oak-hickory uplands so it seems probable that they were present in this latter habitat also. Owing to the small amount of data it cannot be determined if the absence from the spruce-birch-larch swamp had any significance.

Data from the old field clearly showed that the jumping mouse avoided the inner part of the old field where the vegetation was more sparse. All captures were from along the southern edge which bordered a small sedge marsh and where there was an abundance



Fig. 6.—Transect captures of *Zapus hudsonius*.

of grasses and shrubs. This can be attributed either to modification of temperature and/or increased moisture. Data from the marsh showed no relationship between amount of vegetation and abundance of *Z. hudsonius*.

Moisture.—*Z. hudsonius* was found exclusively in moist or wet places. As mentioned above, all captures in the old field were from the more moist areas immediately adjacent to a marshy situation. Data from the marsh (Fig. 7) indicate a slight preference for some standing water although there were fewer captures at those stations with more than 2.5 centimeters of standing water. The transect data showed the most captures on the bog mat which was wet. As a hibernating species, it obviously must pass the winter in the drier areas where the frost line is above the water table. During the remainder of the year, *Z. hudsonius* appears to inhabit the more moist situations.

Food.—Not enough data were obtained to reach any conclusions. This species feeds on green vegetation as well as seeds so that an abundant food supply is available during the spring, summer, and fall. Since the animals are not active during the winter, food probably would not be a limiting factor.

Temperature.—These animals hibernate during the winter and thus are not subjected to exceedingly low temperatures. They avoided the sparse vegetation of the old field which may have been in part a response to higher temperatures. No correlation between temperature and the occurrence of *Z. hudsonius* was observed in the other habitats.

Interspecific competition.—No other species exerted an obvious influence upon the distribution of the jumping mouse. Data from

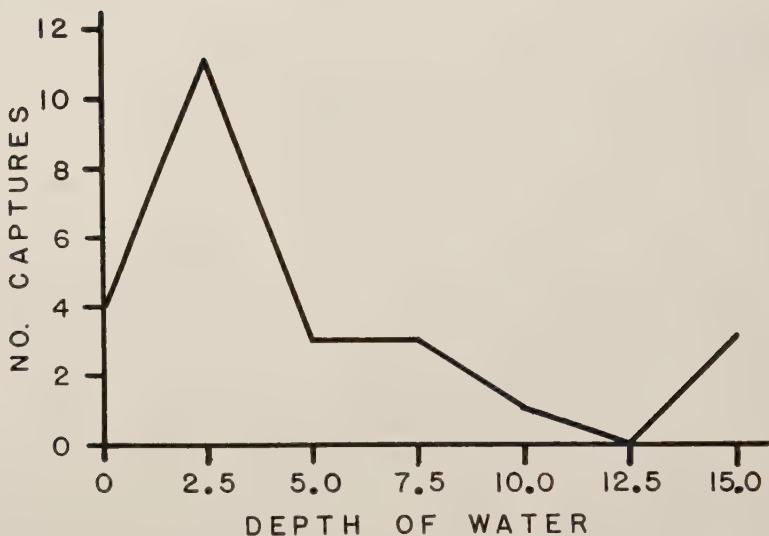


Fig. 7.—Relation of depth of water to captures of *Zapus hudsonius* in a grass-sedge marsh. Water depth in centimeters.

the marsh showed numerous captures at stations that also had numerous *Microtus pennsylvanicus* captures.

Conclusions.—It appears that *Z. hudsonius* occurs only in moist situations. The lowest humidity that it can tolerate has not been determined. In comparison to *Blarina brevicauda* (which has been shown to require an almost completely saturated air; Pruitt, 1959) it is even less abundant in those areas that have low humidities (Getz, 1961a). It, therefore, must be restricted to habitats in which the air is almost completely saturated. Within areas having such a humidity there appears to be no preferred habitat.

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Mating Behavior of the *Peromyscus truei* Species Group of White-Footed Mice

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ABSTRACT: Mice of the *Peromyscus truei* species group (*P. truei*, *P. comanche* and *P. nasutus*) were studied to determine the mating reaction of individuals to members of their own species.

Little intraspecific variation was noted. When the mating pattern was defined, six phases were evident: 1) initiation of courtship by the female; 2) circling of the female before the male; 3) posturing by the female; 4) mounting by the male; 5) thrust-intromission by the male; 6) dismounting by the male.

There is a tendency for pair formation. Interactions such as grooming and genitalia smelling act to condition a mouse to the other's presence, and certain responses, such as the sequence culminating in mating, are given only to those animals with which they have become familiar. Strange animals always elicit responses of an aggressive nature.

INTRODUCTION

This report deals with the results of observations on mating behavior of the species *Peromyscus comanche*, *P. nasutus* and *P. truei* of the *Peromyscus truei* group of mice. These species appear to comprise a natural unit and are presumably genetically more closely related to each other than to members of other species groups. Two species, *P. nasutus* and *P. truei*, are ecologically sympatric over much of their range in mountainous regions of New Mexico and other western states, whereas the allopatric species, *P. comanche*, is limited to canyon floors and slopes of northwestern Texas.

Because of possible differences in mating behavior between the species, attention was focused on observations to determine the mating reaction of individuals to members of their own species. Other purposes of this study were to learn (1) if the female was more important than the male in determining whether copulation occurred; (2) and if she was, at what point in the sequence of mating behavior copulation was permitted.

These observations are presented not as a definitive study but as initial observations on a complicated behavioral sequence, and it is felt that these data should be recorded in the literature, since similar observations have not been reported in any detail.

Acknowledgments.—The author acknowledges John G. Reimann and Alice Louise Baartz for assisting in many aspects of the laboratory work and John A. King and W. Frank Blair for critically reading the manuscript. W. Frank Blair allowed the use of space and equipment in the Vertebrate Speciation Laboratory of The University of Texas, and his cooperation is gratefully appreciated.

METHODS

The mice used in this study consisted of first-generation laboratory descendents of field-caught animals trapped in New Mexico and Texas. Most of these mice had been raised in the Vertebrate Speciation Laboratory for at least a year, and none were less than six months of age when chosen for study. Both males and females were isolated for at least 30 days prior to their use in the observations. Mouse pairs were chosen at random from the stocks available and placed in adjoining compartments of a mating cage. These compartments were connected by a removable wooden tunnel covered with wire mesh. The partition between the two compartments and the side walls and roof of the cage were of quarter-inch mesh and allowed the mice to be aware of each other. As the closed tunnel which separated the two compartments was removed only when observations were made, interactions between the two mice were possible only at that time. Food, nesting material and water were supplied in each compartment.

A male was placed in one compartment and a female in the other. As the displacement of an animal into a strange environment may be a stressful experience (see Southwick, 1959), the usual procedure was to keep the mice in separate compartments for a minimum of 48 hours before observations were begun. Agonistic reactions and excessive motor activity were the usual behavioral responses if they were permitted immediate physical contact. These behavioral reactions were minimized if both mice were given time to adapt to the new environment and become accustomed to the other's presence.

The observational procedure was as follows. The room was darkened at night 30 minutes or more before observations were begun. This period of time was sufficient for the mice to emerge from the nesting material and commence normal nocturnal motor activities. A reflector lamp with a 40 watt red darkroom bulb was placed over the compartments of the cage to be observed, and the observer sat approximately 4 feet from the cage. Although the extent was determined by the behavior of the mice, observations were usually made for a minimum of 20 minutes.

Observations were usually begun at 10:00 P.M. and repeated at one to two hours intervals until copulation was seen. If copulation was not observed by the seventh night, the mice were removed from the cage and replaced by another pair. Clark (1936) reported that

TABLE I.—Mating data obtained in intraspecific pairings of three species of the *Peromyscus truei* species group

Species	Total pairings	Successful pairings	Mean no. of mounts	Mean no. of thrusts	Thrusts per total mounts	Mean no. washings by male	Observation time (in minutes)
<i>comanche</i>	4	2	37.5	31.0	82.7	29.5	190
<i>nasutus</i>	1	1	29.0	25.0	86.2	21.0	85
<i>truei</i>	9	2	10.5	10.5	100.0	8.0	77

the estrus cycle of *Peromyscus maniculatus* females was approximately every 4 to 6 days and that females exhibited breeding condition once during each estrus cycle. Therefore 7 days was considered sufficient to observe estrus if it was to occur.

Fourteen pairings with the 3 species were made, but in only 5 of the pairings was mating behavior seen. Subsequent to each observation a complete account of the behavior of each mouse was recorded. Notes included number of mounts, number of thrusts and washings of the genitalia by the male. These data are summarized in Table I.

GENERAL MATING PATTERN

The mating behavior of the mice in intraspecific pairings was so similar that a general description can be given which is applicable to the three members of the group.

If the female was not in estrus, exploration of the cages was the initial activity after the lights had been extinguished and the tunnel between the compartments had been removed. The mice usually showed no animosity toward each other after a few preliminary encounters and tended to accept the other as a normal component of the environment. Although there was considerable variation between pairs of mice, such activities as mutual grooming and smelling the genitalia, rump and tail of each other were the most frequent interactions.

In several pairings the male appeared to be sexually stimulated when allowed access to the female and would follow and attempt to mount her. If the female was not receptive, she responded in one of several ways. Most frequently she would change to a *defensive posture*, i.e., rear on her hind feet and face the male, her head thrown back and her forepaws held toward her chin. When this posture was taken, the male usually desisted in his efforts and began to explore. Occasionally a female was seen to rotate her body toward the male and snap her jaws toward him. This was frequently accompanied by a short lunge in his direction, and the male would immediately decamp. Not infrequently she would chase him into the adjoining compartment, then resume her investigative activity. If the male was unusually aggressive, these measures were not effective, and she would decamp. Then the male would follow, and a heated chase of short duration would ensue. However, this response was not often observed and was seen only if the male was persistent in his attempts to mount or to smell her genital region.

When the female was in estrus and receptive to the male she placed herself demonstratively before him and initiated a display which normally resulted in copulation. This can be described in the following manner. After the initial contacts between the two individuals had been made, the female evidenced her interest in the male by persistently smelling the scrotum and the base of his tail. The male then turned and smelled the female's genital region. This resulted

in the animals walking in tight circles, their noses to the genital region of the other. After moving in this manner for a short while, the female would then turn away from the male, lower the posterior portion of her body to the floor, and move in tight circles around or in front of the male. In this *circling* display the perineal region of the female was placed in direct contact with the floor of the cage, and the female propelled herself across the floor by movements of the forelimbs. Although in normal locomotion the tail of the animal is held high, the tail of the circling female was held flat to the floor.

If the male was still stimulated, he would follow the female, keeping his nose to the base of her tail or dorsum. Occasionally he might interrupt to smell the floor where she had immediately passed but shortly thereafter would begin to follow her again. The amount of circling by the female varied, but interrupted clock-wise and counter clock-wise movements were common.

Immediately prior to the first copulation the female would cease to circle, extend her body forward and arch her back. This arching was pronounced and usually accompanied by an angling of the tail laterally at its base. Thus the female perineum was raised, and the male would approach from the rear and mount. He extended his body over the female and firmly grasped her in the region of the diaphragm with his forelimbs. Intromission was effected, and at the time of thrust usually one or the other of the male's hind limbs was elevated 2 or 3 millimeters above the floor. Mating was accomplished with a single piston-like stroke of the penis, occasionally of such vigor as to cause the female to lurch forward. Frequently the female was heard to utter a high squeak at the moment of thrust.

After the pelvic thrust the male immediately relaxed his grasp on the female. Then he would throw himself back on his hind legs and tail and begin rapidly to wash the penis, which was withdrawn from the sheath. Washing of the genitalia by the male was regularly but not always seen after each copulation. Although the female *Peromyscus* might wash her perineum after copulation, she most frequently would circle before the washing male, emitting high shrill squeaks as she circled.

Although the frequency and time lapse varied, the duration of union was approximately 0.5 to 2.0 seconds, with shorter periods the most common. Matings occurred rapidly in series from 3 to 10, with the male pausing to groom or rest after each series. During estrus the sex drive of the female rarely lessened, and although the male may have been washing or resting, she would continue to circle before him. The time spent observing the mating pairs was not constant, but as few as 21 and as many as 62 copulations were seen in intra-specific matings. Unless the sex drive of one or the other of the sexes diminished, it was believed that mating occurred at least erratically through the period of darkness until dawn. Mating by one pair was observed as late as 4:45 A.M. when the light of the rising sun began to weakly illuminate the room.

DISCUSSION

When courtship and mating data of the species of the *truci* group are analyzed, a similar pattern consisting of six rather distinct phases is evident.

The first, initiation of courtship, is made by the female, who approaches the male and provides the necessary stimulation conducive to the arousal of the mating pattern. On occasion the mere physical presence of a female was seen to sexually stimulate a male, but if she were in anestrus, stimuli afforded by the male failed to release a reciprocal response. In the male the copulatory threshold, i.e., the stimulation necessary for copulatory activity, varies greatly. A male with a high threshold will ignore a female, even though she may be in estrus, whereas a male with a low threshold will attempt to copulate with an anestrus as well as an estrus female.

The second phase was not mentioned by Svihla (1930) in his general description of the behavior of several species of *Peromyscus*, nor to the author's knowledge has it been described in more recent literature. This phase, the circling display of the female, may or may not take place prior to the first mating but does occur before subsequent matings or series of matings. As this response is released by the female only in the presence of the male, it may be considered as a means by which the female leaves a trail of her sexual condition for the male. In nature it is possible that she might attempt to leave a long continuous trail, so that any male happening upon it would follow her. In the confines of the small cage this trail laying may take the form of circling. Whether circling in the presence of the male in the cage, or laying a long trail in the absence of the male in nature, the stimulus is probably of an olfactory nature. As none of the observations were conducted in more spacious cages, it is not known if circling by the female would be absent from the pattern or if circling is simply an expression of the small cage.

The third phase is posturing by the female. This is characterized by pronounced arching of the back and exposure of the perineum and is a necessary prerequisite for subsequent phases. Prior to the first mating, the second phase may be absent from the mating sequence and the third phase preceded by the first.

The fourth phase, mounting, is initiated by the male. If the female is receptive, the fifth phase, thrust-intromission, follows and consists of a single, rapid thrust of the pelvis by the male. If she is not receptive, she breaks the pattern by decamping. The duration is determined by the male, and the time needed to complete mating is apparently constant in intraspecific matings of the group. The sixth phase, dismounting, is determined by the male. In all matings observed the female maintained her posture until the male had dismounted.

From his careful study of mating behavior in the white rat, Beach (1944) has tentatively concluded that multiple stimulation rather than any particular kind of stimulation is required for arousal of the mating pattern in the male. In other words a combination of olfactory,

tactile, visual and probably other sensations represent the sexually exciting stimulus leading to mating behavior. Evidence from observations of the *truei* group support this. In several observations the male did not respond to the stimuli posed by the female until olfactory and tactile supplemented the visual stimuli. Of the several stimuli essential for the response culminating in copulation, the olfactory appeared to be most important. In all matings the male did not begin his role in the courtship pattern until he had thoroughly smelled the floor of the female's compartment and particularly the genitalia of the estrus female. After initial stimulation of the male, multiple stimuli are probably responsible for a continuance of the mating performance.

Certain data from these observations indicate a tendency for pair formation. Although the mice were usually hostile to each other during the first few contacts, interactions such as nuzzling, grooming and genitalia smelling appeared to be essential for the establishment and continuance of amiable relations. Once begun, these epimeletic activities were continued and acted to condition a mouse to the other's presence. On several occasions when another male was substituted for the original male, the female invariably responded in an antagonistic manner. If in estrus, she never responded to the new male with any of the posturing movements exhibited previously before the familiar male. Likewise if another male were introduced into the compartment with the pair, he was invariably attacked by the resident male. Individual recognition, and subsequent preservation of pair integrity, may well be a fundamental adaptive mechanism as important in *Peromyscus* as in groups of social animals which are closed to other individuals of the same species (see King, 1954).

Certain differences between the mating behavior of these mice and other rodents are apparent. Calhoun (1956) noticed that in *Mus musculus* the male grasped the female by the nape of her neck with his teeth during the union. Likewise he recorded one copulation which lasted as long as 60 seconds. In his work with white rats Stone (1926) noticed a quivering of the ears in female rats when they were mounted, and Stone and Ferguson (1940) recorded from 4 to 8 strokes of the penis by the male rat during copulation. King (1956) recorded a maximum mating time of 2.06 minutes for C57BL/10 inbred mice and observed that after mounting, the male gave several rapid thrusts, becoming slower after intromission, and then becoming passive, frequently falling over on his side.

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Book Reviews

FLORA VAN NEDERLAND. By S. J. Ooststroom. P. Noordhoff, Groningen, Netherlands. 890 pages, 1038 text figures. Fourteenth printing. 1956. Price, bound: f. 11,50, or about \$3, American.

This is a new edition of the well-known Dutch flora by Hendrik Heukels, who died in 1936, now revised by Dr. S. J. van Ooststroom of the Rijksherbarium, Leiden. At the beginning of the book, there is an outline, by Professor J. L. Van Soest, of the 11 phytogeographical districts of Holland, followed by a map, and an outline of classification of plant associations. There is also an illustrated glossary of technical descriptive terms.

Among several keys to families and aberrant genera, there is a general key, one based on the Linnaean system, and one for vegetative characters. All are of the bracket type. The main part of the book consists of a combination of keys and short descriptions. Duration, time of flowering, habitat, geographical origin of the species, if not native, and Dutch vernacular names are indicated. All this information is very compactly arranged in a series of continuous keys. Most pages have two-line drawings at the top. Toward the end of the book, there is an explanation of abbreviations of names of authors, with their dates of birth and death, and their nationality, this being followed by two indices, one to Dutch names and the other to botanical names.

Some aspects of the taxonomy in this book are likely to be unfamiliar to most American botanists. Archegoniatae and Gymnospermae are accorded modern phylogenetic treatment, but the sequence of families of Angiospermae is less usual. The sequence begins with Dicotyledons, which are divided into Choripetalae (families 18-98), and Sympetalae (99-137). "Amentiferae" come first, with the families Betulaceae, Fagaceae, etc., following in general the Engler sequence up to Caryophyllaceae, then come Euphorbiaceae, etc., followed by Hamamelidaceae (Fam. 40). Ranunculaceae are the 46th family. Violaceae follow Cruciferae. Guttiferae include Hypericaceae. Rosaceae are kept intact, but legumes fall into two families: Mimosaceae, and Papilionaceae, the latter consisting of the two subfamilies, Caesalpinoideae and Papilionatae. Sympetalae begin with Plumbaginaceae and Primulaceae. Ericaceae and Empetraceae are closely associated. Cucurbitaceae and Adoxaceae are left in the usual position according to Engler. Monocotyledons begin with Alismataceae (so-spelled), followed by Liliaceae, Cyperaceae, Gramineae, and Orchidaceae. The last and presumably most highly evolved and specialized families of Monocotyledons are Sparganiaceae and Typhaceae.

While this book appears to be an excellent practical manual for study of the flora of Holland, the underlying system of classification, not original in this book, leaves much to be desired. It is far from phylogenetic, and could, in fact, be termed retrogressive. It is a very dubious improvement over the archaic but familiar Englerian scheme, and in the Dicotyledons at least, is not at all likely to supersede it.—GEORGE NEVILLE JONES, University of Illinois.

ORCHIDS OF PERU. By Charles Schweinfurth. Fieldiana: Botany, volume 30, number 1, 260 pp., 45 text figures, 1 map. Published by Chicago Natural History Museum, April 9, 1958.

This attractive and useful study, by Mr. Charles Schweinfurth, Research Fellow in the Ames Orchid Herbarium, Botanical Museum, Harvard University, is described as the first attempt at a detailed, systematic account of the

orchids of any Andean region. It was prepared in the Orchid Herbarium of Oakes Ames, the largest and most up-to-date of its kind in the world, at the suggestion of Mr. J. Francis Macbride, as part of his comprehensive *Flora of Peru*. Although it is customary to review botanical works after they have been completed, in this instance it may be appropriate and desirable to draw attention to this important monograph in its present stage of publication.

This monograph is based on the collections of pioneer explorers, including Ruiz & Pavon, and on the modern collections of Macbride, Weberbauer, F. W. Pennell, Llewellyn Williams, Killip, A. C. Smith, Ferreyra, Vargas, and several others. These materials have been supplemented by loans of specimens from the Gray Herbarium, New York Botanical Garden, United States National Herbarium, and the Chicago Natural History Museum. Types, or photographs or drawings of types, have been studied from the Lindley Herbarium at Kew, and the Reichenbach Herbarium in Vienna.

Peru is rich in the number of species of orchids, and when all that are known to occur there have been accounted for, there will be about 900 species in 120 genera. The species are arranged alphabetically and described in detail. Many of them are beautifully illustrated by Gordon Dillon. The work includes all binomials attributed to the Peruvian orchid flora, which means that there is a relevant bibliography for each species. Specimens are cited on a definite geographical basis. The framework of the taxonomy is the enumeration of the orchids of Peru (1921) by Rudolph Schlechter. The author modestly attributes the systematic treatment and the theoretical viewpoints implied as having been derived from his long association with the great orchidologist, Oakes Ames. There is also an expression of deep appreciation to his Harvard colleagues, Dr. A. F. Hill, and Dr. R. E. Schultes.

This is a notable taxonomic work, of interest and use not only to orchid specialists, but to botanists and horticulturists in both the New World and the Old. To taxonomists, ecologists, and other students of plants in South America generally, and particularly those of the Andean region, the work is to be regarded as a starting point for further studies of floras of the countries adjacent to Peru. Genera familiar to U. S. botanists include *Habenaria*, *Pogonia*, and *Spiranthes*. At least one species, *Habenaria repens*, occurs in southeastern United States, and many others occur in Mexico and West Indies. One statement, that Orchidaceae comprise "between 15,000 and 35,000 members," in the opinion of this reviewer, represents a somewhat generous estimate, but perhaps it is intended to mean that when all species of Orchidaceae have been discovered, described, and classified, the total number will be far in excess of that which we now comprehend.—GEORGE NEVILLE JONES, University of Illinois.

MUSHROOMS OF THE GREAT SMOKIES. A FIELD GUIDE TO SOME MUSHROOMS AND THEIR RELATIVES. By L. R. Hesler. University of Tennessee Press, Knoxville, xii + 289 pp., 183 figs. 1960. \$5.50.

For its many yearly visitors, excluding a certain type of hit and run tourist, the attractions of the Great Smoky Mountains National Park often approach the hypnotic. Some travelers probably see little more than Newfound Gap and Clingman's Dome, which alone are worth the trip. But a surprisingly large number return year after year. The first mistake these perennial visitors make is to get out of their automobiles and walk into the forests. After such an excursion the case is hopeless. Perhaps, a trip through a laurel slick might effect a cure—certainly it almost kills! However, the only successful treatment is to return as often as possible. A surprising number of these visitors

become interested in the flora and fauna of the Park and many become amateur naturalists.

Another kind of visitor to the Park exists. He is the professional naturalist. The majority of these professionals are rightly concerned with their specialties and responsibilities, but on occasion a rare individual may transcend this outlook and try to explain some facet of this fascinating region to its admirers. Professor Hesler is one of these rare professionals. Dr. Hesler's long residence as Professor of Botany and Dean of Arts and Sciences at the University of Tennessee has enabled him to observe the Park fungi in all seasons, and his interest in these fungi, especially the agarics, has been abiding over the years. His guide is a successful attempt to convey to the amateur some of this large store of knowledge.

Many texts aimed at the interested layman often attempt either too much or too little. Professor Hesler has avoided these twin traps. In Part I a brief discussion of the fungi in relation to the Park is presented. The parts of a mushroom are illustrated and discussed along with the properties of edibility and halucinogenity. Certain phenomena which might confuse or intrigue the amateur such as fairy rings, luminescence, autodigestion, parasitism, and mycorrhiza are also discussed. Part II includes the taxonomic account. One hundred and eighty-three species are treated; an ample number for the beginner. If the amateur's interest is still with him after these, there is appended a short bibliography of available titles to spur him on in his pursuit. Two major keys are included. In the first key are listed the agarics and *Cantharellus*. The conspicuous Ascomycetes, the polypores, the boletes, and *Craterellus* are in the second key. Keys to species are also given. Each of these diagnostic keys are designed to be used with a hand-lens or naked eye, which is an attractive feature to the novice. With a spore-print and fresh specimens, the user should be able to name any of the species included in this guide; a statement which cannot always be made even about keys designed for professional use. By reducing technical jargon to a minimum, that bugaboo is avoided. For that irreducible core of terms there is a short glossary. Each species is excellently illustrated with the author's own photographs and are tastefully arranged to show most of the diagnostic characters. The Kingsport Press is to be congratulated on the reproductions. With each species description there are distributional notes (an inside cover map is included to facilitate discussion), comments on its habitat, and, if necessary, a brief exposition on species with which it might be confused.

While specifically written as a field guide to those mushrooms occurring within the National Park, the book should be useful in adjacent regions. Roughly 25 per cent of the species included in this guide occur even as far south and west as lower Louisiana. The weight, about 1¼ lbs., and dimensions, 8¾ x 5¾ inches, make it easy to carry about in a jacket pocket.

Finally, its dedication to the Park's naturalist, Arthur Stupka, is notably appropriate. Mr. Stupka's knowledge and enthusiasm for Natural History and his vast store of that special kind of patience needed for dealing with amateurs and professionals is immediately recognized by those who come into contact with him.—A. L. WELDEN, Tulane University, New Orleans.

EVOLUTION: ITS SCIENCE AND ITS DOCTRINE. Edited by T. W. M. Cameron. University of Toronto Press (for the Royal Society of Canada). 1960. xi + 242 pp. 24 figs. \$5.00.

This volume consists of twenty papers which were presented at the 1959 meeting of the Royal Society of Canada in commemoration of the centenary

of the publication of the *Origin of Species* by Charles Darwin. Many such commemorative volumes have appeared, but this is among the better ones. The first six papers deal with geological and paleontological aspects of evolution. In the first essay, Russell discusses several examples of polyphyletic ancestry of major groups, and he believes that the establishment of such is one of the major contributions of paleontology to evolutionary theory. In an essay on the Lower Cambrian fauna, Okulitch gives data which show that, contrary to the impressions of many who are not specialists on the Lower Cambrian, the known fauna of the *early* Cambrian was not particularly rich. A highlight of his paper is a brief discussion of the Archeocyatha, an exclusively Cambrian phylum described only a few years ago by Okulitch. As few zoologists are familiar with this phylum, a more extensive treatment would have been welcome.

The next six papers discuss biological aspects of evolution, beginning with an elementary statement of its genetic basis by Thompson. The most original papers in this section are those of Dunbar on the evolution of stability and of Savile on the significance of barrier penetration.

A group of five papers on philosophical and sociological aspects of evolution is headed by the only French paper in the volume, *Quelques Réflexions Philosophiques sur la Science de l'Évolution*, par le R. P. Louis-Marie Régis. Finally, there is a group of three papers on cosmic evolution. Particularly noteworthy here is a paper on the origin of the elements by Cameron, one of the major architects of the current theory of the continuous origin of the elements.

Selection of a few papers for comment from such a series is always difficult. Another reviewer—or this reviewer at another time—might well have chosen quite a different group of papers for comment. The papers are inevitably uneven in interest and readability, but every student of evolution will find much to reward his perusal of this volume.—EDWARD O. DODSON, University of Ottawa, Ottawa 2, Ontario.

THE BIOLOGY OF WEEDS. Edited by John L. Harper. Charles C. Thomas, Springfield, Illinois. 1960. 256 p. Illus. \$9.75.

For the purpose of this first symposium volume of the British Ecological Society weeds have been defined "as higher plants which are a nuisance." This definition, more precise than Emerson's "A plant whose virtues have not yet been discovered" and less laconic than the moralist's "Tobacco," serves to unify a diverse group of plant species of various habits, which in one way or another interfere with human activities. Because of this, the study of weeds has usually been restricted to applied botany, agriculture and control methods; and, as the Introduction to this volume notes, "pure botanists" have avoided these "camp followers of cultivation." The content of this volume explicitly excludes chemical controls from the biology of weeds and except for a few passing references this exclusion has been adhered to, the symposium concerning itself solely with the origins, taxonomy, distribution and ecology, physiology, genetics and evolution of plants which happen to be weeds.

The volume contains twenty-five short papers which are grouped into six sections. The first section, which is not titled includes articles on "The history of weeds in Britain," "Some reflections on the ecology of weeds" and "Patterns of change within grassland communities." The remaining five sections are headed: "Problems in the taxonomy and evolution of weeds,"

"The dormancy and dispersal of weed seeds"; "Population studies, interference and competition"; "Special weed problems" and "Autecological studies on weed species." Most of the authors represent British institutions although several German and one Dutch worker have contributed papers.

While it is not unexpected that the articles included should be varied in quality and interest the general level is good. The topics covered are too varied for easy summarization. Of particular interest in the first section were the late glacial and pre-human existence of weed species and the utilization of weeds as food plants by early man. Some of these are the progenitors of our modern crop plants; others, though used earlier, have fallen from favor and are now outcasts. The observations of H. Lieth of the wanderings of clones within a community in his experiments are striking.

In the second part the attributes of weedy and non-weedy plants are compared and specific taxonomic problems of *Polygonum*, *Viola*, *Hypericum* and *Euphorbia* species considered. The third section includes discussions of the effect of herbicides and root exudates of crop plants on dormancy and germination, the association of weeds and crop seeds, and the effect of husbandry on the seed population. In the fourth section density effects on seed production and population interactions are considered. Specific weeds, *Acacia* in Africa, gorse (known previously to this reviewer only from the misfortunes of Pooh Bear) in New Zealand, water hyacinth in the Sudan and the parasitic *Loranthaceae* in Ceylon are considered in the fifth section. The sixth and last section includes considerations of the autecology of specific weedy species with interesting examples of biological control in polders and the effect of a change in the eating habits of the British public upon the spread of *Nardus stricta* in pastures.

This symposium volume illustrates many fascinating biological problems which are provided by weeds and, however much of a nuisance they may be to the agriculturalist, they should be of great interest to the "pure" botanist.

-ROBERT P. MCINTOSH, University of Notre Dame.

Notes and Discussion

Checklist of American Amphibians and Reptiles

The American Society of Ichthyologists and Herpetologists announces the preparation of a new edition of the Society sponsored *Checklist of American Amphibians and Reptiles*. The new checklist will have a completely revised format with greater detail than any previous edition, will be a loose-leaf publication, and will be authored by many specialists. As the need for revision arises, new individual pages will be published to supplant the original ones. The preparation of the new list is under the guidance of a checklist committee. The chairman and editor is William J. Riemer, Florida State Museum, Flint Hall, University of Florida, Gainesville.

The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

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Vol. 66, 1961

(July, October)

PUBLISHED BY THE UNIVERSITY OF NOTRE DAME

NOTRE DAME, INDIANA

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The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 66

JULY, 1961

No. 1

Life-Forms of Kentucky Flowering Plants

DOROTHY GIBSON

Chicago Natural History Museum, Chicago 5, Illinois

ABSTRACT: A study was made of the vegetative structures of all reported species of Kentucky flowering plants, in order to determine the percentage distribution of species among the assigned life-forms, and in hope of stimulating further research in this field. Species were tabulated according to duration, life-form (Raunkiaer) and extended scheme (Turrill), and the biological spectrum obtained from summarizing these tabulations was compared with Raunkiaer's "normal" spectrum and the spectra of other known regions. In addition to reflecting Kentucky's high percentage of hemicryptophytes, the study reveals considerable variation in growth habit behavior within a species, indicates the usefulness of such criteria in the determination of plant communities, and points up the need for detailed studies of community relationships.

Life-forms are assumed to be the result of each plant's evolutionary morphological adjustment to its environment. A variety of vegetative structures have developed, by natural selection, enabling plants to function in harmony with environmental changes. This study attempts to establish the kinds and degrees of protection afforded the perennating buds of Kentucky plants during the unfavorable season; to determine the percentage distribution of species among the assigned life-forms, and to compare the resulting biological spectrum with Raunkiaer's "normal" spectrum and the spectra of other regions.

The historical review of physiognomic and epharmonic systems of classification outlined by Sr. Elizabeth Seton MacDonald in her paper, "The life-forms of the flowering plants of Indiana" (1937), adequately presents accounts of the various systems and methods and will therefore not be repeated here. Raunkiaer's system, based upon the position on the plant of rejuvenating organs, has been followed, and the species are classified according to Turrill's "extended scheme" of duration and external characteristics.

When this study was initiated, it was realized that more than one climatic type often occurs within the boundary of a state. However, it was hoped that a series of such state studies would at least show the changing form-trend or gradient as controlled by temperature, atmospheric precipitation, and soils. The resulting spectra of the same general climate types do reflect the same broad patterns of life-form types (Tables II and III), supporting the premise that there is a correlation of life-forms and environments. However, the spectra are most useful in bringing out features for investigation as they point up the facts that one form cannot be singled out as indicative of an

environment, and that life-forms are in part the result of the floral composition of the unit being studied, and of the history of that floral unit. The complexities of such relationships cannot be shown by simple comparative lists, and I am convinced that only by many unit studies in the field, leading to a series of zone studies based on dominant species and frequency data as suggested by Cain (1945), can the situation be accurately expressed. Although this approach is unfortunately impracticable at present for many, I believe it is the only way that we can eventually arrive at a true picture of edaphic conditions and prevailing phytoclimates, as well as original natural areas. (In this connection it is hoped that collectors will realize that specimen labels containing more information as to dominant plants in the associations of each habitat would permit the construction of more useful spectra.)

As this study progressed, it became increasingly apparent that more variation in growth habit behavior exists than is generally known or has been reported. A species may have more than one life-form in accordance with habitat, age, or other factor. A specimen of *Stellaria pubera* (usually appearing as a chamaephyte) collected by Dr. E. Lucy Braun was an upright proto-hemicryptophyte; *Cirsium vulgare*, wintering as an obvious semi-rosette, also produces root-buds on a horizontal rhizome. *Arabis perstellata*, a semi-rosette type, was found by Braun (1956) to be perennial by means of a slowly elongating central axis. Hemicryptophytes which are able to produce runners or stolons do not always do so. Eight species of *Viola* which had produced runners were collected in Kentucky and were so reported from Connecticut by Ennis (1928). However, five of these eight species collected in Indiana were found to be without runners (MacDonald, 1937). Some plants behave variously as annuals, biennials, or even triennials. *Sedum pulchellum*, an obviously perennial chamaephyte in limestone soil in Edmonson County, Kentucky, appears in Jessamine County, also in limestone soil, as a biennial (Braun 1984 and 920, private collection).

Factors other than light or temperature may be much more important in the establishment of plant associations in various habitats. The fact that many geophytes, especially among the monocotyledons, bloom very early before shade is furnished by the forest environment, indicates that the forest habitat is necessary for other reasons — perhaps symbiotic fungal relationships, as in the case of the later blooming *Monotropa hypopithys*, a root-bud geophyte, which is also an epiparasite by way of a mycorrhiza which is in turn dependent on forest tree roots (Björkman, 1959). A study of life-forms emphatically points up the need for detailed study of community relationships. It is not enough to know that certain synusiae exist in certain habitats — we need to know why they are where they are and the answers must lie in many carefully planned seasonal field studies of smaller ecological units.

Specific names used in this study are essentially those listed by Braun (1943) and, with certain exceptions, McFarland (1942). The

species omitted are those represented by specimens which could not be checked, as specimens lost when fire destroyed the herbarium of the University of Kentucky were not all duplicated in other herbaria. When a name has been reduced to synonymy since these lists appeared, and when the later revision is generally recognized, the revised nomenclature has been used. A few species reported since 1943 which were available for examination have been added and are annotated. Previously unreported species are also annotated and are indicated as new state records by double asterisks. Naturalized species (indicated by a single asterisk), which are included in the distributional summary in Table I, are also summarized by family, following the systematic list (Table VI). Species which have been observed to vary in duration or form are included in parentheses in the summaries preceding each group. In addition, Table V was prepared to compare the percentage distribution of woody types, parasites and saprophytes, aquatics, and herbaceous twining plants. The following symbols are used in the tabulations and summaries:

- B. T — Tree. Sh — Shrub. (4) — Perennial. (2) — Biennial. (1) — Annual.
- C. Ph — Phanerophytes:
 MM — Mega- Meso- Phanerophytes (Bud-heights 8 to 30 m or more)
 M — Micro-Phanerophytes (Bud-heights 2 to 8 m)
 N — Nano- Phanerophytes (Bud-heights below 2 m)
 Ch — Chamaephytes
 H — Hemicryptophytes
 Hp — Proto-Hemicryptophytes without runners.
 Hs — Semi-Rosette without runners.
 Hr — Rosette without runners.
 Hpr — Proto-Hemicryptophytes with runners.
 Hsr — Semi-Rosettes with runners.
 Hrr — Rosette with runners.
 Cr — Cryptophytes
 G — Geophytes
 Grh — Rhizome
 Gst — Stem-tuber
 Grt — Root-tuber
 Gb — Bulb
 Gr — Root-bud
 Gp — Root-parasites
 HH — Helo-, Hydrophytes
 Th — Therophytes
 S — Stem Succulents
 E — Epiphytes
- D. 1. Evergreen tree.
 2. Deciduous tree.
 3. Evergreen shrub.
 4. Deciduous shrub.
 5. Woody liana or sprawler.
 7. Plant with spines, thorns, or strong prickles.
 9. Perennial herb, or sub-shrub, partially woody at base, with aerial parts dying back but not to ground level.
 10. Grasses and grass-like plants.

- | | |
|--|---|
| 11. Rush and sedge forms
with suppressed leaves.
12. Perennial herbs and sub-
shrubs with runners, or
sprawling, ascending, or
herbaceous or suffruti-
cose stems.
14. Rosette plants.
15. Herbaceous twining plants
generally dying down
each year. | 16. Perennial herbs dying
down yearly with peren-
nial buds on more or
less thick stock at
ground level.
17. Geophytes.
18. Annual herbs.
19. Hydrophytes.
20. Parasites and saprophytes. |
|--|---|

(NOTE: Categories 6 — shrubs, and 13 — cushion plants, were omitted for Kentucky plants.)

TABLE I.—Distributional summary of native and naturalized species

	Fam.	Spp.	Duration		(4)	(2)	(1)
			T	Sh			
Native and naturalized	129	1846	141	174	1149	86	296
Naturalized	37	226	8	9	75	32	102
Native	92	1620	133	165	1074	54	194
			Life-form				
			Ph	Ch	H	Cr	Th
Native and naturalized			300	26	942	282	296
Naturalized			16	3	94	11	102
Native			284	23	848	271	194

In the systematic list, an entry of symbols representing life-form and duration will hold for all subsequent taxa in that family, unless a new entry appears.

Kentucky, an area of 40,598 square miles, lies approximately 38° N. latitude and 85° W. longitude, with altitude ranging from 275 feet to 4,250 feet. That part of the state in the physiographic province of the Interior Low Plateau (Fenneman, 1938) includes the western coal fields, the rugged escarpments of the Highland Rim (mixed deciduous forests, uplands of oak, hickory, and red cedar, pine-covered ridges),

TABLE II.—Biological spectrum of Kentucky, compared with the "normal" spectrum of Raunkiaer and available spectra of other regions

	No. of native spp.	Ph	Ch	H	Cr	Th
Connecticut (Ennis)	1453	15.0	1.9	49.4	21.7	11.7
Olympic Peninsula (Jones)	1015	11.0	6.0	52.0	22.0	9.0
Illinois (Hansen)	1909	15.5	1.6	50.2	19.8	12.9
Indiana (MacDonald)	1837	15.3	1.7	50.3	19.6	13.0
Kentucky	1620	17.6	1.4	52.6	16.6	11.8
Normal spectrum		46.0	9.0	26.0	6.0	13.0

the fertile bluegrass, and the karst regions to the south. The eastern section, in the Appalachian Highlands, includes part of the unglaciated Allegheny Plateau, and the mixed mesophytic forests of the Cumberland Mountains and the Cumberland Plateau. The mean annual temperature for the state is 56° F.; annual rainfall averages 45 inches, and there are normally about 180 days each year without frost.

In this favorable climate, Kentucky's native hemicryptophytes surpass those of Indiana and Illinois by over two per cent (Table II). The percentage of native phanerophytes, also more than two per cent higher than that of the neighboring states to the north, was to be expected. The prevailing temperature, humidity, and length of growing season favor these two groups, the herbaceous layer being controlled to some extent by the canopy layer. There is little doubt that during glaciation, the slopes and ravines of the forests along the northern boundary provided refugia for northern species, while the

TABLE III.—Comparisons of biological spectra of various regions, including introduced species

	No. of native and natural- ized species	(MM	Ph M	N)
Cape Breton (Ennis)	637	4.3	3.7	6.1
Connecticut (Ennis)	1622	5.4	5.6	3.5
New York (Taylor)	1907	4.5	7.2	3.5
Illinois (Hansen)	2071		(13.9)	
Indiana (MacDonald)	2109	5.8	5.5	3.0
Kentucky	1846	6.3	6.8	3.2
Piedmont, N. C. (Oosting)	387		(29.7)	
North Carolina—Tenn., Smoky Mtns. (Cain)	1142	8.9	6.1	4.5
Alabama (Ennis)	2012	7.7	4.6	4.7
Mississippi (Ennis)	1724	8.9	4.6	4.2

	No. of native and natural- ized species	Ch	H	Cr (G	HH)	Th
Cape Breton (Ennis)	637	1.8	51.3	15.3	10.3	6.7
Connecticut (Ennis)	1622	2.0	49.4	12.6	7.7	13.5
New York (Taylor)	1907	5.3	33.3	20.2	11.7	13.0
Illinois (Hansen)	2071	2.0	47.5	(17.1)		14.4
Indiana (MacDonald)	2109	1.9	49.0	12.6	5.4	16.7
Kentucky	1846	1.4	51.2	12.4	2.9	15.8
Piedmont, N. C. (Oosting)	387	1.6	45.0	(11.3)		12.4
North Carolina—Tenn., Smoky Mtns. (Cain)	1142	1.7	52.1	15.1		11.5
Alabama (Ennis)	2012	3.1	47.8	12.8	4.3	14.4
Mississippi (Ennis)	1724	3.1	49.4	12.4	3.8	12.8

southern species were not displaced. The gray-brown, melanized forest soils which predominate are known for their productivity. Another factor to be considered is that many Kentucky counties have not been adequately collected, some are still botanically unreported, and a greater part of those which have been reported are now or were recently forest regions, favorable to hemicryptophytes.

The fact that Kentucky has a greater percentage of microphanerophytes (Table III) than the states to the north or to the south is understood when we take into account the number of large trees cut in lumbering operations. Also, shrubby plants appearing as nanophanerophytes to the north may here become small trees.

The chamaephyte percentage is only 0.2 per cent less than Illinois and 0.3 per cent less than Indiana. The Kentucky cryptophyte percentage, three per cent less than that of the two northern states, may be explained by pointing out the unusually low helo-hydrophyte count, which normally contributes one-third to one-half of the cryptophyte percentage (also see Table V). This is almost certainly incorrect, as very little collecting has been reported from the many aquatic and semi-aquatic habitats in the state.

The native therophyte population is 1.2 per cent less than that of Indiana and 1.1 per cent less than that of Illinois. When introduced species are included (Table III), the altered therophyte percentage, as expected, shows the greatest increase, surpassed only by that of Indiana. The only acceptable explanation for the high percentage of therophytes in Indiana seems to be that Indiana has been more completely collected and reported.

The Pteridophyte quotient (Pt.-Q.) of Kentucky, summarized in Table IV to express the ratio of spermatophytes to pteridophytes, is compared with spectra available for some other regions. Data for the Pt.-Q. spectra was obtained from McCoy's list (1937), with additions from lists prepared by McFarland (1942), Reed (1958), and Smith (1959). The very high Pt.-Q. of 1.26 per cent is probably due to the fact that the entire region has undergone less climatic change and less soil change during erosion cycles than adjacent regions. The humid

TABLE IV.—Pteridophyte-quotient (Pt.-Q.) of Kentucky and other regions

	Number of native species		Pt.-Q. Ratio
	Spermatophytes	Pteridophytes	
World	140,000	5,600	25:1
Laurentian			
(Marie-Victorin)	1,837	80	1.1
Connecticut (Raunkiaer)			1.3
Illinois (Hansen)	1,681	64	0.95
Indiana (MacDonald)	1,837	58	0.8
Kentucky	1,620	82	1.26
Alabama (Raunkiaer)			0.7
New Mexico (Raunkiaer)			0.3

TABLE V.—Comparisons of native woody types, aquatics, and parasitic plants

	Woody types	Aquatics	Parasites and saprophytes
Connecticut	15.0	8.5	----
Illinois	16.2	5.5	1.4
Indiana	16.5	6.2	.8
Kentucky	18.5	3.2	1.1

forest climax has existed since Tertiary times. Old and relatively undisturbed soils (mull humus of the forests, limestone and shale outcrops, and sandstone soils of plateaus and ridges) are much more favorable to a variety of pteridophytes than are eroded, or new soil types to the north or the alluvial embayment to the south.

Kentucky's diversified topography of mountains, plateaus, river bluffs, and "prairie" grasslands produces highly variable climax and subclimax communities. When this state flora has been completely collected and reported, serious studies of these complex and most interesting ecological compositions should be made.

Acknowledgments.—This problem was suggested to me by the late Dr. Theodor Just of Chicago Natural History Museum, and I was fortunate enough to have his continued interest and guidance during the study. I also wish to express sincere appreciation to Dr. C. Earle Smith, Jr., of Chicago Natural History Museum, for his assistance in reading and criticizing this paper; to Dr. E. Lucy Braun, who allowed me to examine plants in her private herbarium and supplied information regarding certain plants; Dr. Dale M. Smith, of the University of Kentucky; Dr. P. A. Davies, University of Louisville; and to the many other botanists and friends who assisted in numerous ways. I especially wish to thank Miss Ellen Sanders, Taylor County High School, Campbells-ville, Kentucky, and Miss Cleo Watson and Mr. Joseph Watson of Columbia, Kentucky, for their assistance in the field.

SYSTEMATIC LIST

SPERMATOPHYTA

Families: 129. A. Genera: 626. Species: 1,846. Varieties: 266.

B. T—141 (+6). Sh—174 (+4). (4)—1149 (+8). (2)—86 (+11). (1)—296 (+17).

C. MM—114 (+3). M—127 (+4). N—59 (+2). Ch—26(+1). H—942 (+1). G—230 (+1). HH—52 (+1). Th—296 (+6). S—1. E—1.

D. 1—13. 2—136 (+7). 3—16. 4—115 (+2). 5—49(+1). 7—71. 9—8. 10—314 (+1). 11—9. 12—23. 14—75. 15—16. 16—655 (+2). 17—202. 18—296 (+2). 19—30. 20—19.

GYMNOSPERMAE

Families: 2. A. Genera: 5. Species: 8. Varieties: 1.

B. T—7. Sh—1. C. MM—7. N—1. D. 1—6. 2—1. 3—1.

1. *Taxaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 3—1.

Taxus canadensis Marsh.

B. Sh C. N D. 3

2. *Pinaceae*

- A. Genera: 4. Species: 7. B. T—7. C. MM—7. D. 1—6. 2—1.
Pinus strobus L. B. T C. MM D. 1
P. echinata Mill.
P. virginiana Mill.
P. rigida Mill.
Tsuga canadensis (L.) Carr.
Taxodium distichum (L.) L. C. Rich. B. T C. MM D. 2
Juniperus virginiana L. B. T C. MM D. 1
var. *crebra* Gern. and Grisc.

ANGIOSPERMAE

Families: 127. A. Genera: 621. Species: 1838. Varieties: 265.

- B. T—134 (+6). Sh—173 (+4). (4)—1149 (+8). (2)—86 (+11).
(1)—296 (+17).
C. MM—107 (+3). M—127 (+4). N—58 (+2). Ch—26 (+1). H—
942 (+1). G—230 (+1). HH—52 (+1). Th—296 (+6). S—1.
E—1.
D. 1—7. 2—135 (+7). 3—15. 4—115 (+2). 5—49 (+1). 7—71. 9—
8. 10—314 (+1). 11—9. 12—23. 14—75. 15—16. 16—655 (+2).
17—202. 18—296 (+2). 19—30. 20—19.

Monocotyledonae

Families: 19. A. Genera: 137. Species: 463.

- B. Sh—5. (4)—393 (+1). (2)—(1). (1)—65 (+1).
C. M—5. N—2. Ch—1 (+1). H—223 (+1). G—133 (+1). HH—33
(+1). Th—64 (+1).
D. 1—6. 2—1. 3—2. 5—5. 7—5. 9—1. 10—314 (+1). 11—9. 12—1.
14—5. 15—6. 16—28. 17—104. 18—64. 19—15. 20—4.

1. *Typhaceae*

- A. Genera: 1. Species: 2. B (4)—2. C. HH—2. D. 16—2.
Typha latifolia L. B. (4) C. HH D. 16
T. angustifolia L.

2. *Sparganiaceae*

- A. Genera: 1. Species: 2. B. (4)—2. C. HH—2. D. 16—2.
Sparganium angrocladum B. (4) C. HH D. 16
(Engelm.) Morong
S. americanum Nutt.

3. *Potamogetonaceae*

- A. Genera: 1. Species: 7. B. (4)—7. C. HH—7. D. 19—7.
Potamogeton americanus B. (4) C. HH D. 19
Cham. & Schlecht.
P. pectinatus L.
P. diversifolius Raf.
P. foliosus Raf.
var. *macellus* Fern.
P. panormitanus Biv.
P. berchtoldi Fieber
var. *tenuissimus*
(Mert. & Koch) Fern.
P. epiphydrus Raf.

4. *Najadaceae*

- A. Genera: 1. Species: 2. B. (4)—2. C. HH—2. D. 19—2.
Najas guadalupensis B. (4) C. HH D. 19
 (Spreng.) Morong
N. gracillima (A. Br.) Morong

5. *Alismaceae*

- A. Genera: 4. Species: 7. B. (4)—7. C. HH—7. D. 16—7.
Alisma subcordatum Raf. B. (4). C. HH D. 16
Echinodorus radicans
 (Nutt.) Engelm.
Lophotocarpus calycinus
 (Engelm.) J. G. Sm.
Sagittaria graminea Michx.
S. brevirostra Mack. & Bush
S. latifolia Willd.
 var. *obtusata* (Muhl.) Wieg.
S. longirostra (Michx.) J. G. Sm.

6. *Hydrocharitaceae*

- A. Genera: 2. Species: 2. B. (4)—2. C. HH—2. D. 19—2.
Anacharis canadensis B. (4) C. HH D. 19
 (Michx.) Planch.
Vallisneria americana Michx.

7. *Gramineae*

- A. Genera: 57. Species: 182. B. (4)—130 (+1). (2)—(1). (1)—52.
 C. N—1. Ch—(1). H—115. G—14. Th—52.
 D. 10—182. 12—1. 18—52.
Arundinaria gigantea B. (4) C. N (Ch) D. 10
 (Walt.) Chapm.
Bromus latiglumis B. (4) C. Hs D. 10
 (Shear.) Hitchc.
B. purgans L. var.
laeviglumis (Scribn.) Swallen
 **B. inermis* Leyss. B. (4) C. Hsr. D. 10
 **B. secalinus* L. B. (1) C. Th D. 10, 18
 **B. commutatus* Schrad.
 var. *apricorum* Simonkai
 **B. japonicus* Thunb.
 **B. arvensis* L.
 **B. sterilis* L.
 **B. tectorum* L.
Festuca octoflora Walt.
 var. *tenella* (Willd.) Fern.
 **F. elatior* L. B. (4) C. Hs. D. 10
F. obtusa Spreng.
F. paradoxa Desv.
Glyceria acutiflora Torr.
G. septentrionalis Hitchc.
G. melicaria (Michx.) F. T. Hubb.
G. striata (Lam.) Hitchc.
Poa chapmaniana Scribn. B. (1) C. Th D. 10, 18
 **P. annua* L.
 **P. compressa* L. B. (4) C. Hsr D. 10
P. pratensis L. B. (4) C. Grh D. 10
P. cuspidata Nutt. B. (4) C. Hsr. D. 10

* <i>P. trivialis</i> L.				
<i>P. alsodes</i> A. Gray	B. (4)	C. Hs	D. 10	
<i>P. nemoralis</i> L.				
<i>P. languida</i> Hitchc.				
<i>P. sylvestris</i> A. Gray				
<i>P. autumnalis</i> Muhl.				
<i>Eragrostis reptans</i> (Michx.) Nees	B. (1)	C. Th	D. 10, 18	
* <i>E. megastachya</i> (Koel.) Link				
(Meade County—Davies, 1955.				
Univ. Louisville Herbarium)				
<i>E. hypnoides</i> (Lam.) BSP.				
<i>E. capillaris</i> (L.) Nees				
<i>E. frankii</i> C. A. Mey.				
* <i>E. pilosa</i> (L.) Beauv.				
<i>E. pectinacea</i> (Michx.) Nees				
* <i>E. cilianensis</i> (All.) Link				
<i>E. hirsuta</i> (Michx.) Nees	B. (4)	C. Hs	D. 10	
<i>E. spectabilis</i> (Pursh) Steud.				
<i>Diarrhena americana</i> Beauv.	B. (4)	C. Grh	D. 10	
<i>Uniola latifolia</i> Michx.	B. (4)	C. Hsr	D. 10	
<i>U. laxa</i> (L.) BSP.				
* <i>Dactylis glomerata</i> L.	B. (4)	C. Hs	D. 10	
<i>Melica mutica</i> Walt.				
<i>M. nitens</i> (Scribn.) Nutt.				
<i>Schizachne purpurascens</i>				
(Torr.) Swallen				
<i>Triodia flava</i> (L.) Smyth	B. (4)	C. Hsr	D. 10	
* <i>Agropyron repens</i> (L.) Beauv.	B. (4)	C. Grh	D. 10	
<i>A. smithii</i> Rydb.				
<i>Elymus villosus</i> Muhl.	B. (4)	C. Hs	D. 10	
<i>E. canadensis</i> L.				
<i>E. riparius</i> Wieg.				
<i>E. virginicus</i> L.				
var. <i>australis</i> (Scribn.				
& Ball) Hitchc.				
var. <i>submuticus</i> Hook.				
var. <i>glabriflorus</i> (Vasey) Bush				
var. <i>intermedius</i> (Vasey) Bush				
<i>Hystrix patula</i> Moench				
<i>Hordeum jubatum</i> L.	B. (4), (2)	C. Hs	D. 10	
<i>H. pusillum</i> Nutt.	B. (1)	C. Th	D. 10, 18	
* <i>Lolium perenne</i> L.	B. (4)	C. Hs	D. 10	
* <i>L. multiflorum</i> Lam.	B. (1)	C. Th	D. 10, 18	
* <i>L. temulentum</i> L.				
<i>Sphenopholis obtusata</i>				
(Michx.) Scribn.	B. (4)	C. Hs	D. 10	
<i>S. intermedia</i> (Rydb.) Rydb.				
<i>S. nitida</i> (Spreng.) Scribn.				
<i>Deschampsia flexuosa</i> (L.) Trin.				
* <i>Arrhenatherum elatius</i> (L.) Beauv.				
* <i>Holcus lanatus</i> L.				
<i>Danthonia spicata</i> (L.) Beauv.				
<i>D. compressa</i> Austin				
<i>D. sericea</i> Nutt.				

Calamagrostis canadensis

(Michx.) Beauv.

C. cinnoides (Muhl.) Bart.**Agrostis alba* L. B. (4) C. Hsr D. 10*A. palustris* Huds.*A. eliottiana* Schultes B. (1) C. Th D. 10, 18*A. hyemalis* (Walt.) BSP.

B. (4) C. Hs D. 10

A. perennans (Walt.) Tuckerm.*Cinna arundinacea* L.**Alopecurus carolinianus* Walt. B. (1) C. Th D. 10, 18**Phleum pratense* L.

B. (4) C. Hs D. 10

Muhlenbergia cuspidata

(Torr.) Rydb.

M. sobolifera (Muhl.) Trin. B. (4) C. Hsr D. 10*M. tenuiflora* (Willd.) BSP.*M. racemosa* (Michx.) BSP.*M. mexicana* (L.) Trin.*M. sylvatica* Torr.*M. schreberi* Gmel. B. (4) C. Hs D. 10*M. capillaris* (Lam.) Trin.*Sporobolus asper* (Michx.) Kunth*S. clandestinus* (Spreng.) Hitchc.*S. vaginiflorus* (Torr.) Wood B. (1) C. Th D. 10, 18*S. neglectus* Nash*S. poiretii* (R. & S.) Hitchc.*Brachyelytrum erectum*

(Schreb.) Beauv.

B. (4) C. Hsr. D. 10

Oryzopsis racemosa

(J. E. Sm.) Ricker

B. (4) C. Grh D. 10

Stipa avenacea L.

B. (4) C. Hs D. 10

Aristida dichotoma Michx.

B. (1) C. Th D. 10, 18

A. oligantha Michx.*A. ramossissima* Engelm.*A. longespica* Poir.*A. purpurascens* Poir. B. (4) C. Hs D. 10*A. affinis* (Schult.) Kunth

B. (1) C. Th D. 10, 18

Leptochloa filiformis (Lam.) Beauv.**Eleusine indica* Gaertn.**Cynodon dactylon* (L.) Pers.

B. (4) C. Hsr D. 10

Spartina pectinata Link

B. (4) C. Grh D. 10

Gymnopogon ambiguus

(Michx.) BSP.

B. (4) C. Hsr D. 10

Bouteloua curtipendula

(Michx.) Torr.

**Anthoxanthum odoratum* L.

B. (4) C. Hs D. 10

**Phalaris canariensis* L.

B. (4) C. Grh D. 10

P. arundinacea L.*Leersia lenticularis* Michx.

B. (4) C. Hsr D. 10

L. oryzoides (L.) Sw.*L. virginica* Willd.*Zizania aquatica* L. B. (1) C. Th D. 10, 18*Zizaniopsis miliacea* (Michx.)

Döll & Aschers.

B. (4) C. Grh D. 10

**Digitaria sanguinalis* (L.) Scop.

B. (1) C. Th D. 10, 18

D. ischaemum (Schreb.) Muhl.

- D. violascens* Link
D. filiformis (L.) Koel.
Paspalum fluitans (Ell.) Kunth ~ B. (4) C. Hs D. 10
P. repens Berg.
P. pubiflorum Rupr.
 var. *glabrum* Vasey
P. floridanum Michx.
 var. *glabratum* Engelm.
P. longepedunculatum LeConte
P. setaceum Michx.
P. pubescens Muhl.
P. laeve Michx.
P. circulare Nash
Panicum depauperatum Muhl.
P. linearifolium Scribn.
P. wernerii Scribn.
P. xalapense HBK.
P. microcarpon Muhl.
P. dichotomum L.
P. meridionale Ashe
P. barbulatum Michx.
P. yadkinense Ashe
P. lindheimeri Nash
P. huachucae Ashe
 var. *fasciculatum* (Torr.)
 F. T. Hubb.
P. tennesseense Ashe
P. villosissimum Nash
P. sphaerocarpon Ell.
P. polyanthes Schultes
P. ravenelii Scribn. & Merr.
P. scoparium Lam.
P. ashei Pearson
P. commutatum Schultes
P. clandestinum L.
P. latifolium L.
P. boscii Poir. var. *molle*
 (Vasey) Hitchc. & Chase
P. dichotomiflorum Michx. B. (1) C. Th D. 10, 18
P. flexile (Gattinger) Scribn.
P. gattingeri Nash
P. philadelphicum Bernh.
P. capillare L.
 var. *occidentale* Rydb.
P. virgatum L. B. (4) C. Grh D. 10
P. agrostoides Spreng. B. (4) C. Hs D. 10
P. stipitatum Nash
P. longifolium Torr.
P. anceps Michx. B. (4) C. Grh D. 10
P. verrucosum Muhl. B. (1) C. Th D. 10, 18
Echinochloa crusgalli (L.) Beauv.
 var. *mitis* (Pursh) Peterm.
E. walteri (Pursh) Heller
 **Setaria lutescens*
 (Weigel) F. T. Hubb.

* <i>S. verticellata</i> (L.) Beauv.			
* <i>S. viridis</i> (L.) Beauv.			
* <i>S. italica</i> (L.) Beauv.			
<i>Cenchrus pauciflorus</i> Benth.			
* <i>Miscanthus sinensis</i> Anderss.	B. (4)	C. Hs	D. 10
<i>Erianthus alopecuroides</i> (L.) Ell.			
<i>E. giganteus</i> (Walt.) Muhl.			
* <i>Eulalia viminea</i> (Trin.) Kuntze	B. (1)	C. Th	D. 10, 18
<i>Andropogon scoparius</i> Michx.	B. (4)	C. Hs	D. 10
<i>A. divergens</i> (Hack.) Anderss.			
<i>A. furcatus</i> Muhl.			
<i>A. ternarius</i> Michx.			
<i>A. virginicus</i> L.			
<i>A. glomeratus</i> (Walt.) BSP.			
<i>A. elliotii</i> Chapm.			
* <i>Sorghum halapense</i> (L.) Pers.	B. (4)	C. Grh	D. 10
* <i>S. vulgare</i> Pers.	B. (1)	C. Th	D. 10, 18
<i>Sorghastrum nutans</i> (L.) Nash	B. (4)	C. Grh	D. 10
<i>Tripsacum dactyloides</i> L.			

8. *Cyperaceae*

A. Genera: 11. Species: 125. B. (4)—115. (1)—10.			
C. H—78. Th—10. G.—33 (+1). HH—2 (+1).			
D. 10—118. 11—7. 17—33. 18—10.			
<i>Dulichium arundinaceum</i> (L.) Britt.	B. (4)	C. HH	D. 10
<i>Cyperus flavescens</i> L. var.			
<i>poaeformis</i> (Pursh) Fern.	B. (1)	C. Th	D. 10, 18
<i>C. diandrus</i> Torr.			
<i>C. rivularis</i> Kunth			
<i>C. inflexus</i> Muhl.			
<i>C. esculentus</i> L.	B. (4)	C. Gst	D. 10, 17
<i>C. erythrorhizos</i> Muhl.	B. (1)	C. Th	D. 10, 18
<i>C. strigosus</i> L.	B. (4)	C. Gst	D. 10, 17
<i>C. refractus</i> Engelm.			
<i>C. retrofractus</i> (L.) Torr.			
<i>C. dipsaciformis</i> Fern.			
<i>C. hystericinus</i> Fern.			
<i>C. cylindricus</i> (Ell.) Britt.			
<i>C. ovularis</i> (Michx.) Torr.			
<i>Kyllinga pumila</i> Michx.	B. (1)	C. Th	D. 10, 18
<i>Scirpus americanus</i> Pers.	B. (4)	C. HH	D. 10
<i>S. validus</i> Vahl	B. (4)	C. HH	D. 11
<i>S. atrovirens</i> Muhl.			
var. <i>georgianus</i> Harper	B. (4)	C. Hsr	D. 10
<i>S. polyphyllus</i> Vahl			
<i>S. lineatus</i> Michx.			
<i>S. cyperinus</i> (L.) Kunth			
<i>Eleocharis acicularis</i> (L.) R. & S.	B. (4)	C. Grh	D. 11, 17
<i>E. obtusa</i> (Willd.) Schultes	B. (1)	C. Th	D. 11, 18
<i>E. engelmanni</i> Steud.			
<i>E. calva</i> Torr.	B. (4)	C. Grh	D. 11, 17
<i>E. tenuis</i> (Willd.) Schultes			
var. <i>verrucosa</i> Svenson			
<i>E. compressa</i> Sulliv.			
<i>Fimbristylis autumnalis</i> (L.) R. & S.	B. (1)	C. Th	D. 10, 18
var. <i>mucronulata</i> (Michx.) Fern.			

Bulbostylis capillaris (L.) C. B.Clarke var. *crebra* Fern.*Rynchospora glomerata* (L.) Vahl*R. corniculata* (Lam.) Gray*Scleria triglomerata* Michx.*S. oligantha* Michx.*S. ciliata* Michx.*S. pauciflora* Muhl.*Carex retroflexa* Muhl.*C. texensis* (Torr.) L. H. Bailey*C. rosea* Schkuhr*C. convoluta* Mack.*C. radiata* (Wahl.) Dew.*C. cephalophora* Muhl.*C. leavenworthii* Dew.*C. mesochorea* Mack.*C. muhlenbergii* Schkuhr*C. plana* Mack.*C. gravida* Bailey*C. aggregata* Mack.*C. sparganioides* Muhl.*C. annectens* Bickn.*C. vulpinoidea* Michx.*C. stipata* Muhl.*C. uberior* (C. Mohr) Mack.*C. laevivaginata* (Kükenth.) Mack.*C. crus-corvi* Shuttlw.*C. conjuncta* Boott*C. incompta* Bickn.*C. bromoides* Schkuhr*C. muskingumensis* Schwein.*C. scoparia* Schkuhr*C. projecta* Mack.*C. normalis* Mack.*C. festucacea* Schkuhr*C. brevior* (Dew.) Mack.*C. albolutescens* Schwein.*C. tribuloides* Wahlenb.*C. cristatella* Britton*C. leptalea* Wahlenb.*C. jamesii* Schwein.*C. artitecta* Mack.*C. emmonsii* Dew.*C. communis* Bailey*C. pennsylvanica* Lam.*C. umbellata* Schkuhr*C. hirtifolia* Mack.*C. eburnea* Boott*C. meadii* Dew.*C. plantaginea* Lam.*C. careyana* Torr.*C. platyphylla* Carey*C. digitalis* Willd.*C. purpurifera* Mack.

B. (4)	C. Hpr	D. 10
B. (4)	C. Hp	D. 10
B. (4)	C. Grh	D. 10, 17

B. (4)	C. Hs	D. 10
B. (4)	C. Hsr	D. 10
B. (4)	C. Hs	D. 10

B. (4)	C. Grh	D. 10, 17
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B. (4)	C. Hs	D. 10
B. (4)	C. Grh	D. 10, 17
B. (4)	C. Hs	D. 10

B. (4)	C. Hsr	D. 10
B. (4)	C. Hs	D. 10

B. (4)	C. Grh	D. 10, 17
B. (4)	C. Hsr	D. 10
B. (4)	C. Grh	D. 10, 17

B. (4)	C. Hs	D. 10
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- C. laxiflora* Lam.
 var. *serrulata* Hermann
C. striatula Michx.
C. leptonervia Fern.
C. albursina Sheld.
C. blanda Dew.
C. gracilescens Steud.
C. granularis Muhl.
 var. *recta* Dew.
C. oligocarpa Schkuhr
C. hitchcockiana Dew.
C. amphibola Steud.
 var. *turgida* Fern.
C. glaucodea Tuckerm.
C. gracillima Schw. B. (4) C. Grh D. 10, 17
C. prasina Wahlenb. B. (4) C. Hs D. 10
C. davisii Schwein & Torr. B. (4) C. Grh D. 10, 17
C. aestivalis M. A. Curtis B. (4) C. Hs D. 10
C. debilis Michx.
 var. *rudgei* Bailey
C. allegheniensis Mack.
C. swanii (Fern.) Mack.
C. virescens Muhl.
C. hirsutella Mack. B. (4) C. Grh D. 10, 17
C. caroliniana Schwein.
C. scabrata Schwein. B. (4) C. Hsr D. 10
C. shortiana Dew. B. (4) C. Hs D. 10
C. deamii Hermann
C. buxbaumii Wahlenb. B. (4) C. Hsr D. 10
C. torta Boott B. (4) C. Hs D. 10
C. gynandra Schwein. B. (4) C. Hsr D. 10
C. crinita Lam.
C. stricta Lam.
C. hystricina Muhl.
C. comosa Boott B. (4) C. Hs D. 10
C. frankii Kunth B. (4) C. Hsr. D. 10
C. squarrosa L. B. (4) C. Hs D. 10
C. typhina Michx.
C. lurida Wahlenb.
C. baileyi Britton
C. grayii Carey
C. intumescens Rudge
C. louisianica L. H. Bailey B. (4) C. Grh, HH
 D. 10, 17
C. lupulina Muhl. B. (4) C. Hsr D. 10
C. lupuliformis Sartwell
C. gigantea Rudge
C. willdenowii Schk.
 (Harlan County — Anderson,
 1947. IA)
Cymophyllus fraseri (Andr.) Mack.
9. *Araceae*
- A. Genera: 4. Species: 6. B. (4)—6. C. G—3. HH—3. D. 16—3. 17—3.
Acorus calamus L. B. (4) C. HH D. 16
Orontium aquaticum L.

<i>Arisaema dracontium</i> (L.) Schott	B. (4)	C. Gst	D. 17
<i>A. triphyllum</i> (L.) Schott			
<i>A. atrorubens</i> (Ait.) Blume			
<i>Peltandra virginica</i> (L.) Kunth	B. (4)	C. HH	D. 16

10. *Lemnaceae*

A. Genera: 3. Species: 3. B. (4)—3. C. HH—3. D. 19—3.			
<i>Spirodela polyrhiza</i> (L.) Schleid.	B. (4)	C. HH	D. 19
<i>Lemna minor</i> L.			
<i>Wolffia punctata</i> Griseb.			

11. *Xyridaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 14—1.			
<i>Xyris torta</i> J. E. Smith	B. (4)	C. Hr	D. 14

12. *Commelinaceae*

A. Genera: 2. Species: 7. B. (4)—5. (1)—2. C. H—4. Grh—1. Th—2. D. 16—4. 17—1. 18—2.			
<i>Commelina communis</i> L.	B. (1)	C. Th	D. 18
<i>C. diffusa</i> Burm. f.			
<i>C. elegans</i> HBK.	B. (4)	C. Hp	D. 16
<i>C. virginica</i> L.	B. (4)	C. Grh	D. 17
<i>Tradescantia caliculata</i> Raf.	B. (4)	C. Hp	D. 16
<i>T. subaspera</i> Ker			
<i>T. virginiana</i> L.			

13. *Pontederiaceae*

A. Genera: 2. Species: 3. B. (4)—3. C. HH—3. D. 16—2. 19—1.			
<i>Heteranthera limosa</i> (Sw.) Willd.	B. (4)	C. HH	D. 19
<i>H. reniformis</i> R. & P.	B. (4)	C. HH	D. 16
<i>Pontederia cordata</i> L.			

14. *Juncaceae*

A. Genera: 2. Species: 17. B. (4)—16. (1)—1. C. H—11. G—5. Th—1. D. 10—15. 11—2. 18—1.			
<i>Juncus bufonius</i> L.	B. (1)	C. Th	D. 11, 18
<i>J. effusus</i> L.			
var. <i>solutus</i> Fern. & Wieg.	B. (4)	C. Hr	D. 11
<i>J. macer</i> S. F. Gray	B. (4)	C. Hr	D. 10
<i>J. coriaceus</i> Mack.	B. (4)	C. Hs	D. 10
<i>J. marginatus</i> Rostk.			
<i>J. biflorus</i> Ell.	B. (4)	C. Grh	D. 10
<i>J. torreyi</i> Cov.	B. (4)	C. Gst	D. 10
<i>J. canadensis</i> J. Gay	B. (4)	C. Grh	D. 10
<i>J. subcaudatus</i> (Engelm.) Cov. & Blake			
<i>J. diffusissimus</i> Buckl.	B. (4)	C. Hs	D. 10
<i>J. brachycarpus</i> Engelm.	B. (4)	C. Grh	D. 10
<i>J. acuminatus</i> Michx.	B. (4)	C. Hs	D. 10
<i>J. debilis</i> A. Gray			
<i>Luzula caroliniae</i> S. Wats.	B. (4)	C. Hsr	D. 10
<i>L. multiflora</i> (Ehrh.) Lejeune	B. (4)	C. Hs	D. 10
<i>L. multiflora</i> X <i>echinata</i> var. <i>mesochorea</i>			
<i>L. echinata</i> (Small) Herm.			
var. <i>mesochorea</i> Herm.			

15. *Liliaceae*

A. Genera: 22. Species: 51. B. Sh—5. (4)—46. C. M—5. Ch—1. H—2. G—43. D. 3—1. 5—5. 7—5. 9—1. 15—2. 17—37.			
<i>Chamaelirium luteum</i> (L.) Gray	B. (4)	C. Grh	D. 17

<i>Stenanthium gramineum</i> (Ker) Kunth	B. (4)	C. Gb	D. 17
<i>S. robustum</i> Wats.			
<i>Veratrum parviflorum</i> Michx.	B. (4)	C. Grh	D. 17
<i>V. woodii</i> Robbins			
<i>Uvularia grandiflora</i> J. E. Sm.			
<i>U. perfoliata</i> L.			
<i>U. sessilifolia</i> L.			
* <i>Hemerocallis fulva</i> L.			
<i>Allium tricoccum</i> Ait.	B. (4)	C. Gb	D. 17
* <i>A. vineale</i> L.			
<i>A. canadense</i> L.			
<i>A. cernuum</i> Roth			
<i>Nothoscordum bivalve</i> (L.) Britt.			
<i>Lilium philadelphicum</i> L.			
<i>L. superbum</i> L.			
<i>L. canadense</i> L.			
<i>L. michiganense</i> Farw.			
<i>Erythronium albidum</i> Nutt.			
<i>E. americanum</i> Ker			
<i>Camassia scilloides</i> (Raf.) Cory			
* <i>Ornithogalum umbellatum</i> L.			
<i>Yucca filamentosa</i> L.	B. (4)	C. Ch	D. 9
* <i>Asparagus officinalis</i> L.	B. (4)	C. Grh	D. 17
<i>Clintonia umbellulata</i> (Michx.) Morong			
<i>Smilacina racemosa</i> (L.) Desf. var. <i>cylindrata</i> Fern.			
<i>Disporum maculatum</i> (Buckl.) Britt.			
<i>D. lanuginosum</i> (Michx.) Nichols			
<i>Streptopus roseus</i> Michx. var. <i>perspectus</i> Fassett			
<i>Polygonatum biflorum</i> (Walt.) Ell.			
<i>P. pubescens</i> (Willd.) Pursh			
<i>P. canaliculatum</i> (Muhl.) Pursh			
<i>Medeola virginiana</i> L.			
<i>Trillium sessile</i> L.			
<i>T. hugeri</i> Small			
<i>T. luteum</i> (Muhl.) Harbison			
<i>T. recurvatum</i> Beck			
<i>T. erectum</i> L.			
<i>T. gleasoni</i> Fern.			
<i>T. grandiflorum</i> (Michx.) Salisb.			
<i>T. nivale</i> Riddell			
<i>T. undulatum</i> Willd.			
<i>Aietris farinosa</i> L.			
<i>Smilax pulverulenta</i> Michx.	B. (4)	C. Hpr	D. 15
<i>S. herbacea</i> L. var. <i>lasioneura</i> (Hock) A.DC.			
<i>S. ecirrhata</i> (Engelm.) Wats.	B. (4)	C. Grh	D. 17
<i>S. glauca</i> Walt.	B. Sh	C. M	D. 5, 7
<i>S. bona-nox</i> L.			
<i>S. rotundifolia</i> L. var. <i>quadrangulata</i> (Muhl.) Wood			
<i>S. hispida</i> Muhl.			
<i>S. laurifolia</i> L.	B. Sh	C. M	D. 3, 5, 7

16. *Amaryllidaceae*

- A. Genera: 3. Species: 3. B. (4)—3. C. G—3. D. 17—3.
Hymenocallis occidentalis
 (LeConte) Kunth B. (4) C. Gb D. 17
Agave virginica L.
Hypoxis hirsuta (L.) Cov.
 var. *leptocarpa* (Engelm. & Gray)
 Brackett B. (4) C. Gst D. 17

17. *Dioscoreaceae*

- A. Genera: 1. Species: 4. B. (4)—4. C. G—4. D. 15—4, 17—4.
Dioscorea villosa L. B. (4) C. Grh D. 15, 17
D. hirticaulis Bartlett
D. glauca Muhl.
D. quaternata (Walt.) Gmel.

18. *Iridaceae*

- A. Genera: 3. Species: 7. B. (4)—7. C. H—3. G—4. D. 16—3, 17—4.
Iris verna L. B. (4) C. Grh D. 17
I. cristata Ait.
I. virginica L.
 var. *shrevei*
 (Small) E. Anders.
 **Belamcanda chinensis* (L.) DC.
Sisyrinchium albidum Raf. B. (4) C. Hsr D. 16
S. angustifolium Mill
S. graminoides Bickn.

19. *Orchidaceae*

- A. Genera: 16. Species: 32. B. (4)—32. C. H—9. G—23. D. 14—4.
 16—5. 17—19. 20—4.
Cypripedium calceolus L.
 var. *pubescens* (Willd.) Correll B. (4) C. Grh D. 17
C. acaule Ait.
Orchis spectabilis L. B. (4) C. Grt D. 17
Habenaria flava (L.) Gray
H. clavellata (Michx.) Spreng.
H. cristata (Michx.) R. Br.
H. ciliaris (L.) R. Br.
H. blephariglottis (Willd.) Hook.
 var. *integrilabia* Correll
H. lacera (Michx.) R. Br.
H. psycodes (L.) Spreng.
H. peramoena Gray
Cleistis divaricata (L.) Ames B. (4) C. Gr D. 17
Triphora trianthophora (Sw.) Rydb. B. (4) C. Grt D. 17
Isotria verticillata (Willd.) Raf. B. (4) C. Gr D. 17
Spiranthes beckii Lindl. B. (4) C. Hr D. 14
S. gracilis (Bigel.) Beck
S. vernalis Engelm. & Gray B. (4) C. Hs D. 16
S. lucida (H. H. Eaton) Ames
S. ovalis Lindl.
S. cernua (L.) Richard
Listera smallii Wiegand
Goodyera pubescens (Willd.) R. Br. B. (4) C. Hrr D. 14
Calopogon pulchellus (Sw.) R. Br. B. (4) B. Gst D. 17
Corallorrhiza wisteriana Conrad B. (4) C. Grh D. 17, 20
C. odontorrhiza (Willd.) Nutt.

C. maculata Raf.*C. striata* Lindl.*Malaxis unifolia* Michx.

B. (4) C. Gst D. 17

Liparis liliifolia (L.) Richard

B. (4) C. Hr D. 14

Tipularia discolor (Pursh) Nutt.

B. (4) C. Gst D. 17

Hexalectris spicata (Walt.) Barnh.

B. (4) C. Grh D. 17

Aplectrum hyemale (Muhl.) Torr.

B. (4) C. Gst D. 17

Dicotyledonae

Families: 108. A. Genera: 484. Species: 1375.

B. T—134 (+6). Sh—168. (4)—756 (+7). (2)—86 (+10). (1)—231 (+16).

C. MM—107 (+3). M—122 (+4). N—56 (+2). Ch—25. H—724. G—98. HH—19. Th—232 (+5). S—1. E—1.

D. 1—1. 2—134 (+7). 3—12. 4—115 (+2). 5—44 (+1). 7—66. 9—7. 12—22. 14—70. 15—10. 16—630 (+2). 17—98. 18—232 (+2). 19—15. 20—15.

20. *Saururaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 16—1.

Saururus cernuus L.

B. (4) C. HH D. 16

21. *Salicaceae*

A. Genera: 2. Species: 15. B. T—10 (+1). Sh—5. C. MM—8 (+1). M—5 (+2). N—2 (+2). D. 2—10 (+1). 4—5.

**Populus alba* L.

B. T C. MM D. 2

P. heterophylla L.*P. candicans* Ait*P. deltoides* Marsh.

B. T C. MM D. 2

P. grandidentata Michx.*Salix nigra* Marsh.**S. fragilis* L.*S. caroliniana* Michx.

B. T C. M (N) D. 2

**S. alba* L.

B. T C. MM (M) D. 2

S. interior Rowlee

B. T C. M D. 2

S. discolor Muhl.

B. Sh (T) C. M (N)

D. 4 (2)

S. sericea Marsh.

B. Sh C. N D. 4

S. humilis Marsh.var. *microphylla* (Anderss.) Fern.*S. rigida* Muhl.

B. Sh C. M D. 4

**S. purpurea* L.22. *Myricaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 4—1

Comptonia peregrina (L.) Coult.

B. Sh C. N D. 4

23. *Juglandaceae*

A. Genera: 2. Species: 10. B. T—10. C. MM—10. D. 2—10.

Juglans nigra L.

B. T C. MM D. 2

J. cinerea L.*Carya illinoensis* (Wang.) K. Koch*C. cordiformis* (Wang.) K. Koch*C. ovata* (Mill.) K. Koch*C. laciniata* (Michx. f.) Loud.*C. tomentosa* (Lam.) Nutt.*C. glabra* (Mill.) Sweet*C. ovalis* (Wang.) Sarg.var. *obovata* Sarg.var. *obcordata* (Muhl.) Sarg.*C. pallida* (Ashe) Engl. & Graebn.

24. *Betulaceae*

A. Genera: 5. Species: 8. B. T—7 (+1). Sh—1 (+1). C. MM—6. M—2 (+2). D. 2—7 (+1). 4—1 (+1).

<i>Carpinus caroliniana</i> Walt.				
var. <i>virginiana</i> (Marsh.) Fern.	B. T	C. MM (M)	D. 2	
<i>Ostrya virginiana</i> (Mill.) K. Koch				
<i>Corylus americana</i> Walt.	B. Sh, T	C. M	D. 4, 2	
<i>Betula nigra</i> L.	B. T	C. MM	D. 2	
<i>B. lenta</i> L.				
<i>B. lutea</i> Michx. f.				
var. <i>macrolepis</i> Fern.				
<i>B. allegheniensis</i> Britt.				
<i>Alnus rugosa</i> (DuRoi) Spreng.	B. T, Sh	C. M	D. 2, 4	

25. *Fagaceae*

A. Genera: 3. Species: 21. B. T—21. C. MM—21. M—(1). D. 2—21.

<i>Fagus grandifolia</i> Ehrh.	B. T	C. MM	D. 2	
<i>Castanea dentata</i> (Marsh.) Borkh.				
<i>C. pumila</i> (L.) Mill.				
<i>Quercus alba</i> L.				
<i>Q. bicolor</i> Willd.				
<i>Q. muhlenbergii</i> Engelm.				
<i>Q. prinus</i> L.				
<i>Q. montana</i> Willd.				
<i>Q. stellata</i> Wang.				
<i>Q. macrocarpa</i> Michx.				
<i>Q. lyrata</i> Walt.				
<i>Q. phellos</i> L.				
<i>Q. imbricaria</i> Michx.				
X. <i>Q. leana</i> Nutt.				
<i>Q. rubra</i> L.				
<i>Q. velutina</i> Lam.				
<i>Q. palustris</i> Muench.				
<i>Q. shumardii</i> Buckley				
var. <i>schneckii</i> Britt.				
<i>Q. coccinea</i> Muench.				
<i>Q. falcata</i> Michx.				
<i>Q. marilandica</i> Muench.	B. T	C. MM (M)	D. 2	

26. *Ulmaceae*

A. Genera: 3. Species: 9. B. T—8. Sh—1 (+1). C. MM—7. M—2. D. 2—8 (+1). 4—1.

<i>Planera aquatica</i> (Walt.) J. F. Gmel.	B. T	C. M	D. 2	
<i>Ulmus fulva</i> Michx.	B. T	C. MM	D. 2	
<i>U. americana</i> L.				
<i>U. thomasi</i> Sarg.				
<i>U. alata</i> Michx.				
<i>U. serotina</i> Sarg.				
<i>Celtis occidentalis</i> L.				
var. <i>crassifolia</i> (Lam.) Gray				
<i>C. laevigata</i> Willd.				
<i>C. pumila</i> (Muhl.) Pursh				
var. <i>deamii</i> Sarg.	B. Sh, T	C. M	D. 4, 2	
var. <i>georgiana</i> (Small) Sarg.				

27. *Moraceae*

A. Genera: 5. Species: 6. B. T—4. (4)—1. (1)—1. C. MM—4. G—1.
Th—1. D. 2—4. 15—1. 17—1. 18—1.

Morus rubra L.

B. T C. MM D. 2

M. alba L.

var. *tatarica* (L.) Loud.

**Broussonetia papyrifera* (L.) Vent.

Maclura pomifera (Raf.) Schneid.

Humulus americanus Nutt.

B. (4) C. Grh D. 15, 17

**Cannabis sativa* L.

B. (1) C. Th D. 18

28. *Urticaceae*

A. Genera: 5. Species: 7. B. (4)—3. (1)—4. C. G—2. H—1. Th—4.
D. 16—1. 17—2. 18—4.

Urtica chamaedryoides Pursh

B. (1) C. Th D. 18

U. procera Muhl. in Willd.

B. (4) C. Hpr D. 16

Laportea canadensis (L.) Gaud.

B. (4) C. Grh D. 17

Pilea pumila (L.) Gray

B. (1) C. Th D. 18

Boehmeria cylindrica (L.) Sw.

B. (4) C. Grh D. 17

Parietaria pennsylvanica Muhl.

B. (1) C. Th D. 18

P. floridana Nutt.

29. *Loranthaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. E—1. D. 3—1. 20—1.

Phoradendron flavescens

B. Sh C. E D. 3, 20

(Pursh) Nutt.

30. *Santalaceae*

A. Genera: 2. Species: 3. B. Sh—1. (4)—2. C. N—1. Grh—2. D. 4—1.
17—2. 20—1.

Comandra richardsiana Fern.

B. (4) C. Grh D. 17

C. umbellata (L.) Nutt.

Pyrolaria pubera Michx.

B. Sh C. N D. 4, 20

31. *Aristolachiaceae*

A. Genera: 2. Species: 5. B. (4)—5. C. H—3. Grh—2. D. 14—3. 17—2.

Asarum canadense L.

B. (4) C. Hrr D. 14

var. *reflexum* (Bickn.) Robins.

var. *acuminatum* Ashe

A. virginicum L.

A. arifolium Michx.

Aristolochia serpentaria L.

B. (4) C. Grh D. 17

A. durior Hill

32. *Polygonaceae*

A. Genera: 4. Species: 29. B. Sh—1. (4)—15. (1)—13. C. M—1. H—
12. G—1. HH—2. Th—13. D. 5—1. 7—1. 16—14. 17—1. 18—13.

**Rumex acetosella* L.

B. (4) C. Hsr D. 16

R. altissimus Wood

B. (4) C. Hs D. 16

R. verticillatus L.

R. triangulivalvis (Danser) Rech. f.

**R. crispus* L.

**R. obtusifolius* L.

Polygonum exsertum Small

B. (1) C. Th D. 18

P. erectum L.

P. buxiforme Small

P. aviculare L.

P. tenue Michx.

P. mühlenbergii (Meisn.) Wats.

B. (4) C. Hp D. 16

<i>P. natans</i> A. Eaton	B. (4)	C. HH	D. 16
<i>P. pennsylvanicum</i> L.			
var. <i>laevigatum</i> Fern.	B. (1)	C. Th	D. 18
<i>P. lapathifolium</i> L.			
<i>P. hydropiper</i> L.			
var. <i>projectum</i> Stanford			
<i>P. punctatum</i> Ell.	B. (4)	C. Hp	D. 16
* <i>P. persicaria</i> L.	B. (1)	C. Th	D. 18
<i>P. hydropiperoides</i> Michx.	B. (4)	C. Hp	D. 16
<i>P. setaceum</i> Baldw.	B. (4)	C. HH	D. 16
var. <i>tonsum</i> Fern.			
* <i>P. orientale</i> L.	B. (1)	C. Th	D. 18
<i>P. virginianum</i> L.	B. (4)	C. Grh	D. 17
<i>P. sagittatum</i> L.	B. (1)	C. Th	D. 7, 18
* <i>P. convolvulus</i> L.	B. (1)	C. Th	D. 18
<i>P. dumetorum</i> L.	B. (4)	C. Hp	D. 16
<i>P. scandens</i> L.			
* <i>P. cuspidatum</i> Sieb & Zucc.			
* <i>Fagopyrum esculentum</i> Moench.	B. (1)	C. Th	D. 18
<i>Brunnichia cirrhosa</i> Gaertn.	B. Sh	C. M	D. 5

33. *Chenopodiaceae*

A. Genera: 3. Species: 8. B. (4)—1. (1)—7. C. H—1. Th—7. D. 16—1. 18—7.			
* <i>Chenopodium ambrosioides</i> L.	B. (4)	C. Hp	D. 16
ssp. <i>eu-ambrosioides</i> Aellen			
* <i>C. botrys</i> L.	B. (1)	C. Th	D. 18
<i>C. album</i> L.			
<i>C. hybridum</i> L. var. <i>gigantospermum</i> (Aellen) Rouleau			
* <i>C. murale</i> L.			
<i>C. Standleyanum</i> Aellen			
<i>Atriplex patula</i> L.			
<i>Salsola pestifer</i> A. Nels.			

34. *Amaranthaceae*

A. Genera: 4. Species: 10. B. (4)—1. (1)—9. C. H—1. Th—9. D. 16—1. 18—9.			
* <i>Celosia argentea</i> L.	B. (1)	C. Th	D. 18
* <i>Amaranthus cruentus</i> L.			
* <i>A. hybridus</i> L.			
* <i>A. retroflexus</i> L.			
* <i>A. spinosus</i> L.			
<i>A. blitoides</i> Wats.			
<i>A. graecizans</i> L.			
<i>Acnida tamariscina</i> (Nutt.) Wood			
<i>A. altissima</i> Riddell			
var. <i>subnuda</i> (Wats.) Fern.			
<i>Iresine rhizomatosa</i> Standl.	B. (4)	C. Hp	D. 16

35. *Nyctaginaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. G—1. D. 17—1.			
<i>Oxybaphus nyctagineus</i> (Michx.) Sweet	B. (4)	C. Grt	D. 17

36. *Phytolaccaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. G—1. D. 17—1.			
<i>Phytolacca americana</i> L.	B. (4)	C. Grt	D. 17

37. *Aizoaceae*

- A. Genera: 1. Species: 1. B. (1)—1. C. Th—1. D. 18—1.
**Mollugo verticillata* L. B. (1) C. Th D. 18

38. *Portulacaceae*

- A. Genera: 2. Species: 3. B. (4)—2. (1)—1. C. G—2. Th—1.
 D. 17—2. 18—1.
Claytonia virginica L. B. (4) C. Gst D. 17
C. caroliniana Michx.
**Portulaca oleracea* L. B. (1) C. Th D. 18

39. *Caryophyllaceae*

- A. Genera: 11. Species: 31. B. (4)—13 (+1). (2)—2. (1)—16.
 C. Ch—5 (+1). H—10. Th—16. D. 12—5. 16—10. 18—16.
Stellaria longifolia Muhl. B. (4) C. Ch D. 12
S. pubera Michx. B. (4) C. Ch, Hp D. 12,
 var. *silvatica* (Beguinet) Weath. 16
**S. media* (L.) Cyrill. B. (1) C. Th D. 18
**S. graminea* L.
 (Harlan County — Barbour and
 Barbour, 1950. CU)
S. fontinalis (Short & Peter) Robins. B. (4) C. Ch D. 12
**Cerastium vulgatum* L.
 var. *hirsutum* Fries B. (4), (2) C. Ch D. 12
C. arvense L. B. (4) C. Ch D. 12
**C. viscosum* L. B. (1) C. Th D. 18
**C. nutans* Raf.
**Holosteum umbellatum* L. B. (2) C. Hp D. 16
**Arenaria serpyllifolia* L. B. (1) C. Th D. 18
A. patula Michx.
**Spergula arvensis* L.
Paronychia canadensis (L.) Wood
P. fastigiata (Raf.) Fern.
 var. *paleacea* Fern.
**Agrostemma githago* L.
Silene stellata (L.) Ait.
 var. *scabrella* (Nieuwland)
 Palm. & Steyerl. B. (4) C. Hs D. 16
S. ovata Pursh
**S. cucubalus* Wibel B. (4) C. Hpr D. 16
**S. dichotoma* Ehrh. B. (1) C. Th D. 18
S. antirrhina L.
**S. noctiflora* L.
S. caroliniana Walt.
 var. *wherryi* (Small) Fern. B. (4) C. Hs D. 16
S. regia Sims B. (4) C. Hp D. 16
S. virginica L. B. (4) C. Hs D. 16
S. rotundifolia Nutt.
**Lychnis alba* Mill. B. (2) C. Hs D. 16
**Dianthus armeria* L. B. (1) C. Th D. 18
**D. prolifer* L.
**Saponaria officinalis* L. B. (4) C. Hpr D. 16
**S. vaccaria* L. B. (1) C. Th D. 18

40. *Nymphaeaceae*

- A. Genera: 5. Species: 5. B. (4)—5. C. HH—5. D. 19—5.
Nelumbo lutea (Willd.) Pers. B. (4) C. HH D. 19

Cabomba caroliniana Gray

Brasenia schreberi Gmel.

Nymphaea tuberosa Paine

Nuphar advena Ait.

41. *Ceratophyllaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 19—1.
Ceratophyllum demersum L. B. (4) C. HH D. 19

42. *Ranunculaceae*

A. Genera: 15. Species: 44. B.—Sh—6. (4)—35. (1)—3. C. M—5.
 N—1. H—25. G—10. Th—3. D. 4—1. 5—5. 14—2. 16—23.
 17—10. 18—3.

Hydrastis canadensis L. B. (4) C. Grh D. 17

Isopyrum bitermatum (Raf.) T. & G. B. (4) C. Hsr D. 16

Xanthorhiza simplicissima Marsh. B. Sh C. N D. 4

Actaea pachypoda Ell. B. (4) C. Grh D. 17

Cimicifuga americana Michx.

C. racemosa (L.) Nutt.

Aquilegia canadensis L. B. (4) C. Hs D. 16

**Delphinium ajacis* L. B. (1) C. Th D. 18

D. tricornis Michx. B. (4) C. Hs D. 16

Aconitum uncinatum L. B. (4) C. Hsr D. 16

Anemone quinquefolia L.

var. *interior* Fern. B. (4) C. Grh D. 17

A. caroliniana Walt. B. (4) C. Gst D. 17

A. canadensis L. B. (4) C. Hs D. 16

A. lancifolia Pursh

A. virginiana L.

Anemonella thalictroides (L.) Spach B. (4) C. Grt D. 17

Hepatica acutiloba DC. B. (4) C. Hr D. 14

H. americana (DC.) Ker

Clematis viorna L. B. Sh C. M D. 5

C. pitcheri T. & G.

C. ridgwayi Standl.

C. versicolor Small

C. virginiana L.

Trautvetteria carolinensis

(Walt.) Vail B. (4) C. Grh D. 17

Ranunculus repens L. B. (4) C. Hsr D. 16

**R. acris* L.

(Harlan County — Barbour and
 Barbour, 1950. CU)

B. (4) C. Grh D. 17

**R. bulbosus* L. B. (4) C. Hs D. 16

R. recurvatus Poir.

R. carolinianus DC.

R. septentrionalis Poir. B. (4) C. Hsr D. 16

R. hispidus Michx. B. (4) C. Hs D. 16

R. fascicularis Muhl.

R. abortivus L.

***R. allegheniensis* Britt.

(Gibson 265, Adair County
 — F.)

R. micranthus Nutt.

var. *delitescens* (Greene) Fern.

R. pusillus Poir. B. (1) C. Th D. 18

R. sceleratus L.

<i>Thalictrum clavatum</i> DC.	B. (4)	C. Hs	D. 16
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<i>T. coriaceum</i> (Britt.) Small	B. (4)	C. Grh	D. 17
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<i>T. dioicum</i> L.	B. (4)	C. Hs	D. 16
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<i>T. revolutum</i> DC.			
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<i>T. polygamum</i> Muhl.			
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(Harlan County — Barbour and

Barbour, 1950. CU)

<i>T. dasycarpum</i> Fisch. & Lall.			
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<i>T. perelegans</i> Greene			
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43. *Berberidaceae*

A. Genera: 4. Species: 4.	B. Sh—1.	(4)—3.	C. M—1.	G—3.	D. 4—1.
	7—1.	17—3.			

<i>Podophyllum peltatum</i> L.	B. (4)	C. Grh	D. 17
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<i>Jeffersonia diphylla</i> (L.) Pers.			
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<i>Caulophyllum thalictroides</i>			
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(L.) Michx.

** <i>Berberis thunbergii</i> DC.			
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(Gibson 164, Adair County — F.) B. Sh C. M D. 4, 7

44. *Menispermaceae*

A. Genera: 3. Species: 3.	B. Sh—3.	C. M—3.	D. 5—3.	9—1.
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<i>Menispermum canadense</i> L.	B. Sh	C. M	D. 5, 9
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<i>Cocculus carolinus</i> (L.) DC.	B. Sh	C. M	D. 5
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<i>Calycocarpum lyoni</i> (Pursh) Nutt.			
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45. *Magnoliaceae*

A. Genera 2. Species: 5.	B. T—5.	C. MM—3.	M—2.	D. 2—5.
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<i>Magnolia acuminata</i> L.	B. T	C. M	D. 2
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<i>M. macrophylla</i> Michx.	B. T	C. MM	D. 2
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<i>M. tripetala</i> L.	B. T	C. M	D. 2
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<i>M. fraseri</i> Walt.	B. T	C. MM	D. 2
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<i>Liriodendron tulipifera</i> L.			
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46. *Calycanthaceae*

A. Genera: 1. Species: 1.	B. Sh—1.	C. M—1.	D. 2—1.
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<i>Calycanthus fertilis</i> Walt.	B. Sh	C. M	D. 2
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47. *Anonaceae*

A. Genera: 1. Species: 1.	B. T—1.	C. M—1.	D. 2—1.
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<i>Asimina triloba</i> (L.) Dunal	B. T	C. M	D. 2
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48. *Lauraceae*

A. Genera: 2. Species: 2.	B. T—1.	Sh—1.	C. MM—1.	M—1.	D. 2—1.
	4—1.				

<i>Sassafras albidum</i> (Nutt.) Nees	B. T	C. MM	D. 2
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var. *molle* (Raf.) Fern.

<i>Lindera benzoin</i> (L.) Blume			
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var. *pubescens* Palm. & Steyererm. B. Sh C. M D. 449. *Papaveraceae*

A. Genera: 3. Species: 3.	B. (4)—2.	(2)—1.	C. G—1.	H—2.	D. 16—2.
	17—1.				

<i>Sanguinaria canadensis</i> L.	B. (4)	C. Grh	D. 17
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<i>Stylophorum diphyllum</i>	B. (4)	C. Hs	D. 16
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(Michx.) Nutt.

* <i>Chelidonium majus</i> L.	B. (2)	C. Hs	D. 16
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50. *Fumariaceae*

A. Genera: 3. Species: 5. B. (4)—2. (2)—3. C. G—2. H—3. D. 15—1. 16—2. 17—2.

<i>Dicentra canadensis</i> (Goldie) Walp.	B. (4)	C. Grt	D. 17
<i>D. cucullaria</i> (L.) Bernh.	B. (4)	C. Gb	D. 17
<i>Adlumia fungosa</i> (Ait.) Greene	B. (2)	C. Hs	D. 15
<i>Corydalis sempervirens</i> (L.) Pers.	B. (2)	C. Hs	D. 16
<i>C. flavula</i> (Raf.) DC.			

51. *Cruciferae*

A. Genera: 22. Species: 56. B. (4)—22 (+2). (2)—18 (+6). (1)—16. C. G—10. H—27. Th—17. HH—2. D. 16—27. 17—10. 18—17. 19—2.

* <i>Lepidium campestre</i> (L.) R. Br.	B. (2)	C. Hs	D. 16
<i>L. virginicum</i> L.	B. (2), (1)	C. Hs	D. 16
* <i>L. densiflorum</i> Schrad.			
* <i>Thlaspi arvense</i> L.	B. (1)	C. Th	D. 18
* <i>T. perfoliata</i> L.			
* <i>Alliaria officinalis</i> Andr.	B. (2)	C. Hp	D. 16
* <i>Sisymbrium officinale</i> (L.) Scop.			
var. <i>leiocarpum</i> DC.	B. (1)	C. Th	D. 18
* <i>S. altissimum</i> L.	B. (2)	C. Hs	D. 16
* <i>S. thalianum</i> (L.) J. Gay	B. (1)	C. Th	D. 18
* <i>Brassica campestris</i> L.	B. (2), (1)	C. Hs	D. 16
* <i>B. juncea</i> (L.) Coss.	B. (1)	C. Th	D. 18
* <i>B. kaber</i> (DC.) L. C. Wheeler			
var. <i>pinnatifida</i> (Stokes)			
L. C. Wheeler			
* <i>B. nigra</i> (L.) Koch			
* <i>Barbarea vulgaris</i> R. Br.	B. (4)	C. Hs	D. 16
* <i>B. verna</i> (Mill.) Asch.	B. (4), (2)	C. Hs	D. 16
<i>Iodanthus pinnatifidus</i>	B. (4)	C. Hs	D. 16
(Michx.) Steud.			
<i>Rorippa sessiliflora</i> (Nutt.) Hitchc.	B. (2), (1)	C. Hs	D. 16
<i>R. islandica</i> (Oeder ex Murr.) Borbás			
var. <i>microcarpa</i> (Regel) Fern.			
<i>R. sylvestris</i> (L.) Bess.	B. (4)	C. Hs	D. 16
* <i>Nasturtium officinale</i> R. Br.	B. (4)	C. HH	D. 19
<i>Lesquerella globosa</i> (Desv.) Wats.	B. (2)	C. Hs	D. 16
<i>Armoracea aquatica</i> (Eaton) Wieg.	B. (4)	C. HH	D. 19
<i>Cardamine bulbosa</i> (Schreb.) BSP.	B. (4)	C. Gst	D. 17
<i>C. douglassii</i> (Torr.) Britt.			
<i>C. rotundifolia</i> Michx.	B. (4)	C. Hsr	D. 16
<i>C. pennsylvanica</i> Muhl.	B. (2)	C. Hs	D. 16
<i>C. parviflora</i> L.			
var. <i>arenicola</i> (Britt.) O. E. Schulz			
<i>C. hirsuta</i> (L.) Scop.	B. (1)	C. Th	D. 18
<i>C. flexuosa</i> With.	B. (2)	C. Hs	D. 16
<i>Dentaria laciniata</i> Muhl.	B. (4)	C. Gst	D. 17
<i>D. multifida</i> Muhl.	B. (4)	C. Grh	D. 17
<i>D. multifida</i> X <i>heterophylla</i>			
<i>D. diphylla</i> Michx.			
<i>D. maxima</i> Nutt.			
<i>D. incisa</i> Small	B. (4)	C. Gst	D. 17
<i>D. anomala</i> Eames			

<i>D. heterophylla</i> Nutt.			
<i>Leavenworthia uniflora</i> (Michx.) Britt.	B. (1)	C. Th	D. 18
* <i>Capsella bursa-pastoris</i> (L.) Medic.			
* <i>Camelina sativa</i> (L.) Grantz			
* <i>C. microcarpa</i> Andrz.			
<i>Draba brachycarpa</i> Nutt.			
<i>D. cuneifolia</i> Nutt.			
* <i>D. verna</i> L.			
<i>D. ramosissima</i> Desv.			
var. <i>glabrifolia</i> Braun	B. (4)	C. Hsr	D. 16
<i>Descurainia pinnata</i> (Walt.) Britt.			
var. <i>brachycarpa</i> (Richards.) Fern.	B. (2)	C. Hs	D. 16
<i>Arabis virginica</i> (L.) Poir.			
<i>A. glabra</i> (L.) Bernh.			
<i>A. lyrata</i> L.	B. (4), (2)	C. Hs	D. 16
<i>A. laevigata</i> (Muhl.) Poir.			
var. <i>Burkii</i> Porter	B. (2)	C. Hs	D. 16
<i>A. perstellata</i> Braun			
var. <i>shortii</i> Fern.	B. (4)	C. Hs	D. 16
<i>A. perstellata</i> X <i>A. laevigata</i>			
<i>A. canadensis</i> L.	B. (2)	C. Hs	D. 16
* <i>Erysimum repandum</i> L.	B. (1)	C. Th	D. 18
* <i>Alyssum alyssoides</i> L.			
* <i>Hesperis matronalis</i> L.	B. (2), (4)	C. Hs	D. 16
52. <i>Podostemaceae</i>			
A. Genera: 1. Species: 1. B (4)—1. C. HH—1. D. 19—1.			
<i>Podostemum ceratophyllum</i> Michx.	B. (4)	C. HH	D. 19
53. <i>Crassulaceae</i>			
A. Genera: 2. Species: 3. B. (4)—2 (+1). (2)—1. C. Ch—2. H—1. D. 12—2. 16—1.			
<i>Sedum pulchellum</i> (L.) Scop.	B. (2), (4)	C. Ch	D. 12
<i>S. ternatum</i> Michx.	B. (4)	C. Ch	D. 12
<i>Penthorum sedoides</i> L.	B. (4)	C. Hpr	D. 16
54. <i>Saxifragaceae</i>			
A. Genera: 12. Species: 21. B. Sh—6. (4)—15. C. N—6. H—15. D. 4—4. 5—2. 7—2. 9—3. 14—12. 16—3.			
<i>Astilbe biternata</i> (Vent.) Britt.	B. (4)	C. Hp	D. 16
<i>Boykinia aconitifolia</i> Nutt.	B. (4)	C. Hrr	D. 14
<i>Sullivantia ohionis</i> T. & G.	B. (4)	C. Hr	D. 14
<i>Saxifraga virginienensis</i> Michx.	B. (4)	C. Hrr	D. 14
<i>S. micranthidifolia</i> (Haw.) Britt.	B. (4)	C. Hr	D. 14
<i>S. leucanthemifolia</i> Michx.			
<i>Tiarella cordifolia</i> L.	B. (4)	C. Hrr	D. 14
<i>Heuchera villosa</i> Michx.			
var. <i>macrorrhiza</i> (Small) R., B. & L.	B. (4)	C. Hr	D. 14
var. <i>intermedia</i> R., B. & L.			
<i>H. parviflora</i> Bartl.			
var. <i>rugelii</i> (Shuttlw.) R., B. & L.			
<i>H. puberula</i> Mack. & Bush			
<i>H. americana</i> L.			
var. <i>interior</i> R., B. & L.			
var. <i>brevipetala</i> R., B. & L.			
<i>H. pubescens</i> Pursh			
var. <i>brachyandra</i> R., B. & L.			

<i>H. longiflora</i> Rydb.	B. (4)	C. Hrr	D. 14
<i>Mitella diphylla</i> L.	B. (4)	C. Hsr	D. 16
<i>Parnassia asarifolia</i> Vent.	B. (4)	C. Hs	D. 16
<i>Philadelphus hirsutus</i> Nutt.	B. Sh	C. N	D. 4, 9
<i>P. inodorus</i> L.			
<i>Hydrangea arborescens</i> L.			
var. <i>Deamii</i> St. John			
<i>Itea virginica</i> L.	B. Sh	C. N	D. 4
<i>Ribes cynosbati</i> L.	B. Sh	C. N	D. 5, 7
<i>R. missouriensis</i> (Nutt.) Cov. & Britt.			

55. *Hamamelidaceae*

A. Genera: 2. Species: 2. B. T—1. Sh—1. C. MM—1. M—1. D. 2—1.
4 1.

<i>Hamamelis virginica</i> L.	B. Sh	C. M	D. 4
<i>Liquidambar styraciflua</i> L.	B. T	C. MM	D. 2

56. *Platanaceae*

A. Genera: 1. Species: 1. B. T—1. C. MM—1. D. 2—1.

<i>Platanus occidentalis</i> L.	B. T	C. MM	D. 2
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57. *Rosaceae*

A. Genera: 18. Species: 82. B. T—28. Sh—36. (4)—17. (2)—1.
C. MM—2. M—39. N—9. H—32. D. 2—28. 4—24. 5—12.
7—43. 14—2. 16—16.

<i>Physocarpus opulifolius</i> (L.) Maxim.	B. Sh	C. N	D. 4
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**Spiraea japonica* L.

S. tomentosa L.

var. *rosea* (Raf.) Fern.

Aruncus dioicus (Walt.) Fern.

var. *pubescens* (Rydb.) Fern.

B. (4)	C. Hp	D. 16
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Gillenia stipulata (Muhl.) Trel.

G. trifoliata (L.) Moench.

Malus coronaria (L.) Mill.

B. T	C. M	D. 2
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M. lancifolia Rehd.

Aronia melanocarpa (Michx.) Ell.

B. Sh	C. N	D. 4
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A. prunifolia (Marsh.) Rehder

Amelanchier intermedia Spach

B. T	C. M	D. 2
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A. canadensis (L.) Medic.

***A. arborea* (Michx. f.) Fern.

(Gibson & Watson 321,

Adair County—F)

A. laevis Wiegand.

Crataegus crus-galli L.

B. T	C. M	D. 2, 7
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C. armata Beadle

C. wilkinsonii Ashe

C. engelmannii Sarg.

B. T	C. M	D. 2
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C. punctata Jacq.

B. T	C. M	D. 2, 7
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C. collina Chapm.

C. viridis L.

C. pratensis Sarg.

C. neobushii Sarg.

B. Sh	C. M	D. 4, 7
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C. rubella Beadle

C. boyntonii Beadle

B. T	C. M	D. 2, 7
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C. buckleyi Beadle

C. straminea Beadle

B. Sh	C. M	D. 4, 7
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C. macrosperma Ashe

C. iracunda Beadle

B. T	C. M	D. 2, 7
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<i>C. populnea</i> Ashe				
<i>C. pruinosa</i> (Wendl.) K. Koch	B. Sh	C. M	D. 4, 7	
<i>C. rugosa</i> Ashe				
<i>C. mollis</i> (T. & G.) Scheele	B. T	C. MM	D. 2, 7	
<i>C. coccinioides</i> Ashe	B. T	C. M	D. 2, 7	
<i>C. cibaria</i> Beadle	B. Sh	C. M	D. 4, 7	
<i>C. cibilis</i> Ashe	B. T	C. M	D. 2, 7	
<i>C. uniflora</i> Moench	B. Sh	C. M	D. 4, 7	
<i>C. phaenopyrum</i> (L.f.) Medic.	B. T	C. M	D. 2, 7	
<i>C. calpodendron</i> (Ehrh.) Medic.	B. Sh	C. M	D. 4, 7	
<i>C. pubifolia</i> Ashe				
<i>Rubus odoratus</i> L.	B. Sh	C. Hp	D. 4	
<i>R. occidentalis</i> L.	B. Sh	C. Hpr	D. 5, 7	
* <i>R. phoenicolasius</i> Maxim.	B. Sh	C. Hp	D. 5, 7	
<i>R. hispidus</i> L.	B. Sh	C. Hpr	D. 5, 7	
<i>R. centralis</i> Bailey				
<i>R. flagellaris</i> Willd.				
var. <i>invisus</i> Bailey				
<i>R. baileyanus</i> Britt.				
<i>R. enslenii</i> Tratt.				
<i>R. trivialis</i> Michx.				
<i>R. argutus</i> Link	B. Sh	C. Hp	D. 4, 7	
<i>R. frondosus</i> Bigel.	B. Sh	C. Hp	D. 5, 7	
<i>R. allegheniensis</i> Porter	B. Sh	C. Hp	D. 4, 7	
<i>R. canadensis</i> L.	B. Sh	C. Hpr	D. 5, 7	
<i>R. ostryifolius</i> Rydb.	B. Sh	C. Hp	D. 4, 7	
<i>Fragaria virginiana</i> Duchesne				
var. <i>illinoensis</i> (Prince) Gray	B. (4)	C. Hrr	D. 14	
* <i>Duchesnea indica</i> (Andr.) Focke	B. (4)	C. Hsr	D. 16	
* <i>Potentilla recta</i> L.	B. (4)	C. Hs	D. 16	
<i>P. monspeliensis</i> L.	B. (2)	C. Hs	D. 16	
<i>P. canadensis</i> L.				
var. <i>villosissima</i> Fern.	B. (4)	C. Hsr	D. 16	
<i>P. simplex</i> Michx.				
var. <i>argyrisma</i> Fern.				
<i>Waldsteinia fragarioides</i>				
(Michx.) Tratt.				
var. <i>parviflora</i> (Small) Fern.	B. (4)	C. Hrr	D. 14	
<i>Geum vernal</i> (Raf.) T. & G.	B. (4)	C. Hs	D. 16	
<i>G. canadense</i> Jacq.				
var. <i>grimesii</i> Fern. & Weath.				
<i>G. virginianum</i> L.				
<i>Agrimonia gryposepala</i> Wallr.	B. (4)	C. Hpr	D. 16	
<i>A. rostellata</i> Wallr.				
<i>A. pubescens</i> Wallr.	B. (4)	C. Hp	D. 16	
<i>A. parviflora</i> Ait.	B. (4)	C. Hpr	D. 16	
* <i>Sanguisorba minor</i> Scop.	B. (4)	C. Hs	D. 16	
<i>Rosa setigera</i> Michx.				
var. <i>tomentosa</i> T. & G.	B. Sh	C. M	D. 5, 7	
* <i>R. rubiginosa</i> L.	B. Sh	C. N	D. 5, 7	
* <i>R. micrantha</i> Sm.	B. Sh	C. N	D. 4, 7	
<i>R. palustris</i> Marsh.				
<i>R. carolina</i> L.				
var. <i>villosa</i> (Best) Rehder				
var. <i>glandulosa</i> (Crepin) Rehder				

<i>Prunus americana</i> Marsh.	B. T	C. M	D. 2
<i>P. lanata</i> (Sudw.) Mack. & Bush			
<i>P. angustifolia</i> Marsh.			
var. <i>varians</i> Wight & Hedrick	B. Sh	C. M	D. 4
<i>P. hortulana</i> Bailey	B. T	C. M	D. 2
<i>P. munsoniana</i> Wight & Hedrick			
<i>P. virginiana</i> L.	B. Sh	C. M	D. 4
<i>P. serotina</i> Ehrh.	B. T	C. MM	D. 2
* <i>P. mahaleb</i> L.	B. T	C. M	D. 2

58. Leguminosae

A. Genera: 30. Species: 87. B. T—6 (+1). Sh—5. (4)—56. (2)—5. (1)—15 (+3). C. MM—5. M—3 (+1). N—3. Ch—1. H—56. G—4. Th—15. D. 2—6 (+1). 4—5. 5—1. 7—4. 12—1. 14—3. 15—2. 16—52. 17—4. 18—14.

<i>Schrankia microphylla</i> (Dryand) Britt.	B. (4)	C. Hp	D. 7, 16
<i>Desmanthus illinoensis</i> (Michx.) MacM.	B. (4)	C. Hp	D. 16
<i>Cercis canadensis</i> L.	B. T	C. M	D. 2
<i>Cassia nictitans</i> L.			
var. <i>leiocarpa</i> Fern.	B. (1)	C. Th	D. 18
<i>C. fasciculata</i> Michx.			
var. <i>robusta</i> (Pollard) Macbr.			
<i>C. hebecarpa</i> Fern.			
var. <i>longipila</i> Braun	B. (4)	C. Hp	D. 16
<i>C. marilandica</i> L.			
<i>C. tora</i> L.	B. (1)	C. Th	D. 18
<i>Gleditsia triacanthos</i> L.	B. T	C. MM	D. 2, 7
<i>G. aquatica</i> Marsh.			
<i>Gymnocladus dioica</i> (L.) Koch	B. T	C. MM	D. 2
<i>Cladrastis lutea</i> (Michx. f.) Koch			
<i>Baptisia tinctoria</i> (L.) R. Br.			
var. <i>crebra</i> Fern.	B. (4)	C. Hp	D. 16
<i>B. leucophaea</i> Nutt.			
<i>B. leucantha</i> T. & G.			
<i>B. australis</i> (L.) R. Br.			
* <i>Medicago sativa</i> L.			
* <i>M. lupulina</i> L.	B. (1)	C. Th	D. 18
* <i>M. alba</i> Desr.	B. (2)	C. Hs	D. 16
* <i>M. officinalis</i> (L.) Lam.			
* <i>Trifolium arvense</i> L.	B. (1)	C. Th	D. 18
* <i>T. pratense</i> L.	B. (4)	C. Hr	D. 14
* <i>T. resupinatum</i> L.	B. (1)	C. Th	D. 18
* <i>T. repens</i> L.	B. (4)	C. Hsr	D. 16
* <i>T. hybridum</i> L.	B. (4)	C. Hr	D. 14
* <i>T. reflexum</i> L.			
var. <i>glabrum</i> Lojac	B. (2), (1)	C. Hr	D. 14
* <i>T. agrarium</i> L.	B. (1)	C. Th	D. 18
* <i>T. procumbens</i> L.			
* <i>T. dubium</i> Sibth.			
<i>Psoralea onobrychis</i> Nutt.	B. (4)	C. Hpr	D. 16
<i>P. psoraloides</i> (Walt.) Carey			
var. <i>eglandulosa</i> (Ell.) F. L. Freeman	B. (4)	C. Hp	D. 16
<i>Amorpha fruticosa</i> L.	B. Sh	C. M	D. 4

<i>Petalostemum candidum</i> (Willd.) Michx.	B. (4)	C. Hp	D. 16
<i>P. purpureum</i> (Vent.) Rydb.			
<i>Tephrosia spicata</i> (Walt.) T. & G.			
<i>T. virginiana</i> (L.) Pers.			
<i>Wisteria macrostachya</i> Nutt.	B. Sh	C. M	D. 5
<i>Sesbania exaltata</i> (Raf.) Cory	B. (1)	C. Th	D. 18
<i>Robinia pseudo-acacia</i> L.	B. T	C. MM	D. 2, 7
<i>R. hispida</i> L.	B. Sh, T	C. N, M	D. 4, 2
<i>R. boyntonii</i> Ashe	B. Sh	C. N	D. 4
<i>R. kelseyi</i> Cowell			
<i>Astragalus distortus</i> T. & G.	B. (4)	C. Hp	D. 16
<i>A. canadensis</i> L.			
* <i>Coronilla varia</i> L.	B. (4)	C. Gr	D. 17
<i>Stylosanthes biflora</i> (L.) BSP.	B. (4)	C. Hp	D. 16
var. <i>hispidissima</i> (Michx.) Pollard & Ball			
<i>S. riparia</i> Kearney			
<i>Desmodium pauciflorum</i> (Nutt.) DC.			
<i>D. acuminatum</i> (Michx.) DC.			
<i>D. nudiflorum</i> (L.) DC.			
<i>D. rotundifolium</i> (Michx.) DC.			
<i>D. canescens</i> (L.) DC.			
<i>D. illinoensis</i> Gray			
<i>D. bracteosum</i> (Michx.) DC.			
<i>D. laevigatum</i> (Nutt.) DC.			
<i>D. viridiflorum</i> (L.) Beck			
<i>D. dillenii</i> Darl.			
<i>D. paniculatum</i> (L.) DC.			
var. <i>pubens</i> T. & G.			
<i>D. sessilifolium</i> (Torr.) T. & G.			
<i>D. rigidum</i> (Ell.) DC.			
<i>D. ciliare</i> DC.			
<i>D. marilandicum</i> (L.) DC.			
<i>Lespedeza procumbens</i> Michx.			
<i>L. repens</i> (L.) Bart.			
<i>L. violacea</i> (L.) Pers.			
<i>L. nuttallii</i> Darl.			
<i>L. virginica</i> (L.) Britt.			
<i>L. intermedia</i> (Wats.) Britt.			
<i>L. simulata</i> Mack. & Bush			
<i>L. hirta</i> (L.) Hornem.			
<i>L. capitata</i> Michx.			
* <i>L. cuneata</i> G. Don	B. (1)	C. Th	D. 18
* <i>L. stipulacea</i> Maxim.			
* <i>L. striata</i> (Thunb.) H. & A.			
* <i>Vicia angustifolia</i> Reichard	B. (2), (1)	C. Hp	D. 16
<i>V. caroliniana</i> Walt.	B. (4)	C. Hp	D. 16
* <i>V. villosa</i> Roth	B. (2), (1)	C. Hp	D. 16
<i>Lathyrus palustris</i> L.			
var. <i>myrtifolius</i> (Muhl.) Gray	B. (4)	C. Hp	D. 15
<i>Clitoria mariana</i> L.			
<i>Amphicarpa bracteata</i> (L.) Fern.			
var. <i>comosa</i> (L.) Fern.	B. (4)	C. Hpr	D. 16

<i>Apios americana</i> Medic.	B. (4)	C. Gst	D. 17
<i>A. priceana</i> Robins.			
<i>Galactia volubilis</i> (L.) Britt.			
var <i>mississippiensis</i> Vail	B. (4)	C. Hp	D. 16
<i>Phaseolus polystachyus</i> (L.) BSP.	B. (4)	C. Ch	D. 12
<i>Strophostyles helvola</i> (L.) Britt.	B. (1)	C. Th	D. 18
<i>S. umbellata</i> (Muhl.) Britt.	B. (4)	C. Gr	D. 17
<i>S. leioperma</i> (T. & G.) Piper	B. (1)	C. Th	D. 18

59. *Geraniaceae*

A. Genera: 1. Species: 4.	B. (4)—1.	(1)—3.	C. H—1.	Th—3.
D. 16—1.	18—3.			
<i>Geranium maculatum</i> L.	B. (4)	C. Hsr	D. 16	
<i>G. carolinianum</i> L.	B. (1)	C. Th	D. 18	
* <i>G. columbinum</i> L.				
* <i>G. pusillum</i> Burm. f.				

60. *Oxalidaceae*

A. Genera: 1. Species: 8.	B. (4)—7.	(2)—1.	C. H—7.	G—1.	D. 16—7.
17—1.					
<i>Oxalis montana</i> Raf.	B. (4)	C. Hrr	D. 16		
<i>O. violacea</i> L.	B. (4)	C. Gb	D. 17		
var. <i>trichophora</i> Fassett					
<i>O. grandis</i> Small	B. (4)	C. Hpr	D. 16		
<i>O. repens</i> Thunb.	B. (2)	C. Hpr	D. 16		
<i>O. stricta</i> L.	B. (4)	C. Hp	D. 16		
var. <i>piletocarpa</i> Wieg.					
<i>O. florida</i> Salisb.					
<i>O. europea</i> Jord.	B. (4)	C. Hpr	D. 16		
var <i>Bushii</i> Small					
<i>O. recurva</i> Ell.					
var. <i>macrantha</i> (Trel.) Wieg.					

61. *Linaceae*

A. Genera: 1. Species: 4.	B. (4)—3.	(1)—1.	C. H—3.	Th—1.
D. 16—3.	18—1.			
<i>Linum sulcatum</i> Riddell	B. (1)	C. Th	D. 18	
<i>L. striatum</i> Walt.	B. (4)	C. Hp	D. 16	
<i>L. virginianum</i> L.				
<i>L. medium</i> (Planch.) Trel.				
var. <i>texanum</i> (Planch.) Fern.				

62. *Rutaceae*

A. Genera: 2. Species: 2.	B. T—1 (+1).	Sh—1 (+1).	C. M—2.
D. 2—2 (+1)	4—1 (+1).	7—1.	
<i>Zanthoxylum americanum</i> Mill.	B. T (Sh)	C. M	
	D. 2, 4, 7		
<i>Ptelea trifoliata</i> L.	B. Sh (T)	C. M	D. 4, 2

63. *Simarubaceae*

A. Genera: 1. Species: 1.	B. T—1.	C. MM—1.	D. 2	1.
* <i>Ailanthus altissima</i> (Mill.) Swingle	B. T	C. MM	D. 2	

64. *Polygalaceae*

A. Genera: 1. Species: 10.	B. (4)—3.	(1)—7.	C. H—3.	Th—7.
D. 16—3.	18—7.			
<i>Polygala paucifolia</i> Willd.	B. (4)	C. Hpr	D. 16	
<i>P. polygama</i> Walt.	B. (4)	C. Hp	D. 16	
<i>P. senega</i> L.				
var. <i>latifolia</i> T. & G.				

<i>P. incarnata</i> L.	B. (1)	C. Th	D. 18
<i>P. ambigua</i> Nutt.			
<i>P. cruciata</i> L.			
<i>P. sanguinea</i> L.			
<i>P. nuttallii</i> T. & G.			
<i>P. curtisii</i> Gray			
<i>P. verticillata</i> L.			
var. <i>ambigua</i> (Nutt.) Wood			
var. <i>isocycla</i> Fern.			

65. *Euphorbiaceae*

A. Genera: 6. Species: 22. B. (4)—4. (2)—2. (1)—16 (+2). C. H—5.			
G—1. Th—16. D. 16—17. 17—1. 18—4.			

<i>Phyllanthus caroliniensis</i> Walt.	B. (1)	C. Th	D. 18
<i>Croton glandulosus</i> L.			
var. <i>septentrionalis</i> Muell. Arg.			

<i>C. capitatus</i> Michx.			
<i>C. monanthogynus</i> Michx.			
<i>Crotonopsis elliptica</i> Willd.			
<i>Acalypha ostryaefolia</i> Riddell			
<i>A. rhomboidea</i> Raf.			

<i>A. virginica</i> L.			
<i>A. gracilens</i> Gray			
<i>Tragia cordata</i> Michx.	B. (4)	C. Hp	D. 16
<i>Euphorbia obtusata</i> Pursh	B. (1)	C. Th	D. 18

<i>E. chamaesyce</i> L.			
<i>E. maculata</i> L.			
<i>E. supina</i> Raf.			
<i>E. humistrata</i> Engelm.			
<i>E. marginata</i> Pursh			
<i>E. ipecacuanhae</i> L.	B. (4)	C. Hp	D. 16
<i>E. mercurialina</i> Michx.			
<i>E. corollata</i> L.	B. (4)	C. Grt	D. 17
<i>E. dentata</i> Michx.	B. (1)	C. Th	D. 18
<i>E. heterophylla</i> L.	B. (2), (1)	C. Hp	D. 16
<i>E. commutata</i> Engelm.	B. (2), (1)	C. Hpr	D. 16

66. *Callitrichaceae*

A. Genera: 1. Species: 3. B. (4)—2. (1)—1. C. HH—2. Th—1.			
D. 18—1. 19—2.			

<i>Callitriche deflexa</i> A. Br.			
var. <i>austini</i> (Engelm.) Hegelm.	B. (1)	C. Th	D. 18
<i>C. palustris</i> L.	B. (4)	C. HH	D. 19
<i>C. heterophylla</i> Pursh			

67. *Buxaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 12—1.			
<i>Pachysandra procumbens</i> Michx.	B. (4)	C. Hpr	D. 12

68. *Limnanthaceae*

A. Genera: 1. Species: 1. B. (1). C. Th—1. D. 18—1.			
<i>Floerkea proserpinacoides</i> Willd.	B. (1)	C. Th	D. 18

69. *Anacardiaceae*

A. Genera: 1. Species: 5. B. Sh—5. C. MM—1 (+1). M—3. N—1.			
D. 4—4. 5—1 (+1).			

<i>Rhus typhina</i> L.	B. Sh	C. M	D. 4
<i>R. glabra</i> L.			
<i>R. copallina</i> L.			
var. <i>latifolia</i> Engler			

<i>R. radicans</i> L.	B. Sh	C. MM (N)	D. 5 (4)
<i>R. aromatica</i> Ait.			
var. <i>illinoensis</i> (Greene) Rehder	B. Sh	C. N	D. 4

70. *Aquifoliaceae*

A. Genera: 1. Species: 4. B. T—2. Sh—2. C. M—4. D. 1—1. 2—1.
4—2.

<i>Ilex opaca</i> Ait.	B. T	C. M	D. 1
<i>I. decidua</i> Walt.	B. Sh	C. M	D. 4
<i>I. montana</i> Gray	B. T	C. M	D. 2
<i>I. verticillata</i> (L.) Gray	B. Sh	C. M	D. 4
var. <i>padifolia</i> (Willd.) T. & G.			

71. *Celastraceae*

A. Genera: 3. Species: 6. B. Sh—6. C. MM—1. M—1. N—4. D. 3—1.
4—2. 5—3.

<i>Euonymus atropurpureus</i> Jacq.	B. Sh	C. M	D. 4
* <i>E. europaeus</i> L.	B. Sh	C. N	D. 5
<i>E. americanus</i> L.	B. Sh	C. N	D. 4
<i>E. obovatus</i> Nutt.	B. Sh	C. N	D. 5
<i>Celastrus scandens</i> L.	B. Sh	C. MM	D. 5
<i>Pachistima canbyi</i> A. Gray	B. Sh	C. N	D. 3

72. *Staphyleaceae*

A. Genera: 1. Species: 1. B. Sh—1. C. M—1. D. 4—1.

<i>Staphylea trifolia</i> L.	B. Sh	C. M	D. 4
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73. *Aceraceae*

A. Genera: 1. Species: 6. B. T—6. C. MM—4. M—2. D. 2—6.

<i>Acer negundo</i> L.	B. T	C. MM	D. 2
<i>A. pennsylvanicum</i> L.	B. T	C. M	D. 2
<i>A. spicatum</i> Lam.			
<i>A. saccharum</i> Marsh.	B. T	C. MM	D. 2
var. <i>nigrum</i> (Michx. f.) Britt.			
var. <i>rugelii</i> (Pax) Rehder			
<i>A. saccharinum</i> L.			
<i>A. rubrum</i> L.			
var. <i>trilobum</i> K. Koch			
var. <i>drummondii</i> (H. & A.) Sarg.			

74. *Hippocastanaceae*

A. Genera: 1. Species: 2. B. T—2. C. MM—2. D. 2—2.

<i>Aesculus glabra</i> Willd.	B. T	C. MM	D. 2
<i>A. octandra</i> Marsh.			

75. *Balsaminaceae*

A. Genera: 1. Species: 2. B. (1)—2. C. Th—2. D. 18—2.

<i>Impatiens biflora</i> Walt.	B. (1)	C. Th	D. 18
<i>I. pallida</i> Nutt.			

76. *Rhamnaceae*

A. Genera: 3. Species: 4. B. Sh—4. C. MM—1. M—2. N—1. D. 4—4.
5—1.

<i>Berchemia scandens</i> (Hill) K. Koch	B. Sh	C. MM	D. 4, 5
<i>Rhamnus lanceolata</i> Pursh	B. Sh	C. M	D. 4
<i>R. caroliniana</i> Walt.			
var. <i>mollis</i> Fern.			
<i>Ceanothus americanus</i> L.	B. Sh	C. N	D. 4
var. <i>intermedius</i> (Pursh) Trel.			

77. *Vitaceae*

- A. Genera: 2. Species: 10. B. Sh—10. C. MM—10. D. 5—10.
Vitis labrusca L. B. Sh C. MM D. 5
V. aestivalis Michx.
V. argentifolia Muns.
V. cinerea Engelm.
V. palmata L.
V. vulpina L.
V. riparia Michx.
V. baileyana Muns.
V. rotundifolia Michx.
Parthenocissus quinquefolia
 (L.) Planch.

78. *Tiliaceae*

- A. Genera: 1. Species: 4. B. T—4. C. MM—4. D. 2—4.
Tilia americana L. B. T C. MM D. 2
T. neglecta Spach
T. floridana (V. Engler) Small
T. heterophylla Vent.
 var. *michauxii* (Nutt.) Sarg.

79. *Malvaceae*

- A. Genera: 6. Species: 11. B. (4)—4. (2)—2. (1)—5 (+1). C. H—6.
 Th—5. D. 16—6. 18—5 (+1).
 **Abutilon theophrasti* Medic. B. (1) C. Th D. 18
 **Malva moschata* L. B. (2), (1) C. Hs
 D. 16 (18)
 **M. neglecta* Wallr.
Malvastrum angustum A. Gray B. (1) C. Th D. 18
 **Anoda cristata* (L.) Schlecht.
 **Sida spinosa* L.
Hibiscus militaris Cav. B. (4) C. Hp D. 16
H. moscheutos L.
H. palustris L.
H. lasiocarpus Cav.
 **H. trionum* L. B. (1) C. Th D. 18

80. *Theaceae*

- A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 4—1.
Stewartia ovata (Cav.) Weath. B. Sh C. N D. 4
 var. *grandiflora* Weath.

81. *Hypericaceae*

- A. Genera: 2. Species: 16. B. Sh—5. (4)—9. (1)—2 (+2). C. N—5.
 H—9. Th—2. D. 4—6. 16—9 (+2). 18—2.
Ascyrum stans Michx. B. Sh C. N D. 4
A. hypericoides L.
 var. *multicaule* (Michx.) Fern.
 var. *oblongifolium* (Spach) Fern.
 **Hypericum perforatum* L. B. (4) C. Hp D. 16
H. punctatum Lam. B. (4) C. Hpr D. 16
 var. *pseudomaculatum* (Bush) Fern.
H. frondosum Michx. B. Sh C. N D. 4
H. densiflorum Pursh
H. prolificum L.
H. dolabrisforme Vent. B. (4) C. Hpr D. 16
H. sphaerocarpum Michx.
 var. *turgidum* (Small) Svenson B. (4) C. Hp D. 16

<i>H. denticulatum</i> Walt.			
<i>H. mutilum</i> L.	B. (4), (1) D. 16, 18	C. Hp	
<i>H. canadense</i> L.	B. (4), (1) D. 16, 18	C. Hpr	
<i>H. Drummondii</i> (Grev. & Hook.) T. & G.	B. (1)	C. Th	D. 18
<i>H. gentianoides</i> (L.) BSP.			
<i>H. tubulosum</i> Walt. var. <i>Walteri</i> (Gmel.) Lott	B. (4)	C. Hpr	D. 16
** <i>H. virginicum</i> L. (Gibson and Watson 376, Adair County—F.)			

82. *Cistaceae*

A. Genera: 1. Species: 4. B. (4)—4. C. H—4. D. 16—4.			
<i>Lechea villosa</i> Ell.	B. (4)	C. Hp	D. 16
<i>L. minor</i> L.	B. (4)	C. Hpr	D. 16
<i>L. tenuifolia</i> Michx.	B. (4)	C. Hp	D. 16
<i>L. racemulosa</i> Lam.			

83. *Violaceae*

A. Genera: 2. Species: 43. B. (4)—43. C. H—43. D. 14—37. 16—6.			
<i>Hybanthus concolor</i> (Forster) Spreng.	B. (4)	C. Hp	D. 16
<i>Viola pedata</i> L. var. <i>lineariloba</i> DC.	B. (4)	C. Hr	D. 14
<i>V. pedatifida</i> G. Don			
<i>V. stoneana</i> House			
<i>V. palmata</i> L.	B. (4)	C. Hrr	D. 14
<i>V. egglesonii</i> Brainerd	B. (4)	C. Hr	D. 14
<i>V. triloba</i> Schwein. var. <i>dilatata</i> (Ell.) Brainerd			
<i>V. emarginata</i> LeConte var. <i>acutiloba</i> Brainerd	B. (4)	C. Hrr	D. 14
<i>V. cucullata</i> Ait.			
<i>V. affinis</i> LeConte			
<i>V. papilionacea</i> Pursh	B. (4)	C. Hr	D. 14
<i>V. sororia</i> Willd.			
<i>V. hirsutula</i> Brainerd			
<i>V. fimbriatula</i> J. E. Sm.			
<i>V. sagittata</i> Ait.			
<i>V. lanceolata</i> L.	B. (4)	C. Hrr	D. 14
<i>V. blanda</i> Willd.			
<i>V. primulifolia</i> L.			
<i>V. rotundifolia</i> Michx.			
<i>V. hastata</i> Michx.	B. (4)	C. Hr	D. 14
<i>V. tripartita</i> Ell.			
<i>V. pubescens</i> Ait. var. <i>peckii</i> House			
<i>V. eriocarpa</i> Schwein.			
<i>V. canadensis</i> L.	B. (4)	C. Hs	D. 16
<i>V. striata</i> Ait.			
<i>V. conspersa</i> Reichenb.			
<i>V. rostrata</i> Pursh			
<i>V. walteri</i> House	B. (4)	C. Hrr	D. 14

- V. kitaibeliana* R. & S.
 var. *rafinesquii* (Greene) Fern. B. (4) C. Hr D. 14
V. affinis X *palmata* Dowell
V. affinis X *triloba* Brainerd
V. emarginata X *papilionacea* House
V. hirsutula X *sororia* Dowell
V. hirsutula X *triloba* Brainerd
V. palmata X *sororia* House
V. palmata X *triloba* Brainerd
V. papilionacea X *sororia* Brainerd
V. papilionacea X *stoneana* Brainerd
V. papilionacea X *triloba* Brainerd
V. sagittata X *sororia* Brainerd
V. sororia X *triloba* Brainerd
V. stoneana X *triloba* Brainerd
V. rostrata X *striata* Brainerd B. (4) C. Hr D. 16

84. *Passifloraceae*

- A. Genera: 1. Species: 2. B. (4)—2. C. H—2. D. 15—2.
Passiflora lutea L.
 var. *glabriflora* Fern. B. (4) C. Hp D. 15
P. incarnata L.

85. *Cactaceae*

- A. Genera: 1. Species: 1. B. (4)—1. C. S—1. D. 7—1.
Opuntia compressa (Salisb.) Macbr. B. (4) C. S D. 7

86. *Thymelaeaceae*

- A. Genera: 1. Species: 1. B. Sh—1. C. N—1. D. 4—1.
Dirca palustris L. B. Sh C. N D. 4

87. *Lythraceae*

- A. Genera: 6. Species: 7. B. (4)—3. (1)—4. C. Ch—1. H—1. Th—4.
 HH—1. D. 9—1. 16—2. 18—4.
Ammannia coccinea Rottb. B. (1) C. Th D. 18
A. koehnei Britt.
Didiplis diandra (Nutt.) Wood B. (4) C. HH D. 16
Rotala ramosior (L.) Koehne B. (1) C. Th D. 18
 var. *interior* Fern. & Grisc.
Lythrum alatum Pursh B. (4) C. Hpr D. 16
Cuphea petiolata (L.) Koehne B. (1) C. Th D. 18
Decodon verticillatus (L.) Ell. B. (4) C. Ch D. 9
 var. *laevigatus* T. & G.

88. *Melastomaceae*

- A. Genera: 1. Species: 2. B. (4)—2. C. G—2. D. 17—2.
Rhexia virginica L. B. (4) C. Gr D. 17
R. mariana L.
 var. *leisperma* Fern. & Grisc. B. (4) C. Gr D. 17

89. *Onagraceae*

- A. Genera: 6. Species: 22. B. (4)—14. (2)—7. (1)—1. C. H—18. G—2.
 Th—1. HH—1. D. 16—19. 17—2. 18—1. 19—1.
Jussiaea decurrens (Walt.) DC. B. (4) C. Hp D. 16
J. repens L.
 var. *glabrescens* Ktze. B. (4) C. HH D. 16, 19
 (Meade County — Davies, 1955.
 Univ. Louisville herbarium.)
J. diffusa Forsk. B. (4) C. Hpr D. 16

Ludvigia palustris (L.) Ell.

var. *americana* (DC.)

Fern. & Grisc.

L. alternifolia L. B. (4) C. Hp D. 16

L. glandulosa Walt.

L. hirtella Raf.

Epilobium coloratum Muhl. B. (4) C. Hs D. 16

Oenothera canovirens Steele B. (2) C. Hs D. 16

O. laevigata Bartlett

O. nutans Atkinson & Bartlett

O. pratensis Bartlett

O. pycnocarpa Atkinson & Bartlett

O. laciniata Hill B. (1) C. Th D. 18

O. perennis (L.) Pennell B. (4) C. Hs D. 16

O. tetragona (Roth.) Pennell

var. *longistipata* (Pennell) Munz

var. *fraseri* (Pursh) Munz

var. *brevistipata* (Pennell) Munz

O. speciosa Nutt.

***O. triloba* Nutt. B. (2) C. Hs D. 16

(McFarland 96 — Second Cen-

tury Coll., Fayette County

— F.)

Gaura biennis L.

G. filipes Spach B. (4) C. Hs D. 16

Circaea quadrisulcata (Maxim.)

Franch. & Sav.

var. *canadensis* (L.) Hara B. (4) C. Grh D. 17

C. alpina L.

90. *Haloragidaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 19—1.

Proserpinaca palustris L.

var. *crebra* Fern. & Grisc. B. (4) C. HH D. 19

91. *Araliaceae*

A. Genera: 2. Species: 5. B. Sh—1. (4)—4. C. M—1. H—2. G—2.

D. 4—1. 7—1. 16—2. 17—2.

Aralia nudicaulis L. B. (4) C. Hpr D. 16

A. racemosa L.

A. spinosa L. B. Sh C. M D. 4, 7

Panax quinquefolius L. B. (4) C. Grh D. 17

P. trifolium L.

92. *Umbelliferae*

A. Genera: 24. Species: 35. B. (4)—26. (2) 2 (+1). (1)—7. C. Ch—1.

H—21. G—4. HH—2. Th—7. D. 12—1. 14—1. 16—22. 17—4.

18—7. 19—1.

Hydrocotyle americana L. B. (4) C. Hrr D. 14

Sanicula gregaria Bickn. B. (4) C. Hs D. 16

S. canadensis L. B. (2) C. Hs D. 16

S. trifoliata Bickn. B. (4), (2) C. Hs D. 16

Eryngium yuccaefolium Michx. B. (4) C. Grh D. 17

E. prostratum Nutt. B. (4) C. Ch D. 12

Chaerophyllum procumbens

(L.) Crantz

var. *shortii* T. & G. B. (1) C. Th D. 18

C. tainturieri Hook.

<i>Osmorhiza claytoni</i> (Michx.) Greene	B. (4)	C. Hs	D. 16
<i>O. longistylis</i> (Torr.) DC.			
var. <i>villicaulis</i> Fern.			
* <i>Torilis japonicus</i> (Houtt.) DC.	B. (1)	C. Th	D. 18
<i>Erigenia bulbosa</i> (Michx.) Nutt.	B. (4)	C. Grt	D. 17
* <i>Conium maculatum</i> L.	B. (4)	C. Hs	D. 16
* <i>Bupleurum rotundifolium</i> L.	B. (1)	C. Th	D. 18
<i>Zizia aurea</i> (L.) Koch	B. (4)	C. Hs	D. 16
<i>Z. aptera</i> (Gray) Fern.			
<i>Z. bebbii</i> (Coult. & Rose) Britt.			
<i>Cicuta maculata</i> L.			
<i>Cryptotaenia canadensis</i> (L.) DC.			
<i>Taenidia integerrima</i> (L.) Drude	B. (4)	C. Hp	D. 16
<i>Ptilimnium capillaceum</i> (Michx.) Raf.	B. (1)	C. Th	D. 18
<i>P. nuttallii</i> (DC.) Britt.			
<i>Perideridia americana</i>			
(Nutt.) Reichenb.	B. (4)	C. Grt	D. 17
<i>Sium suave</i> Walt.	B. (4)	C. HH	D. 16
* <i>Aethusa cynapium</i> L.	B. (1)	C. Th	D. 18
<i>Ligusticum canadense</i> (L.) Britt.	B. (4)	C. Hs	D. 16
<i>Thaspium trifoliatum</i> (L.) Gray			
var. <i>flavum</i> Blake			
<i>T. barbinode</i> (Michx.) Nutt.			
var. <i>angustifolium</i> Coult. & Rose			
<i>T. pinnatifidum</i> (Buckl.) Gray			
<i>Angelica curtisii</i> Buckl.			
<i>A. villosa</i> (Walt.) BSP.			
<i>Oxypolis rigidior</i> (L.) Raf.	B. (4)	C. HH	D. 16, 19
* <i>Pastinaca sativa</i> L.	B. (2)	C. Hs	D. 16
<i>Heracleum lanatum</i> Michx.	B. (4)	C. Grt	D. 17
* <i>Daucus carota</i> L.	B. (4)	C. Hs	D. 16

93. *Cornaceae*

A. Genera: 2. Species: 11. B. T—4. Sh—7 (+1). C. MM—3. M—7.
N—1. D. 2—4. 4—7 (+1).

<i>Nyssa aquatica</i> L.	B. T	C. MM	D. 2
<i>N. sylvatica</i> Marsh.			
var. <i>caroliniana</i> (Poir.) Fern.			
<i>Cornus florida</i> L.			
<i>C. alternifolia</i> L. f.	B. T, Sh	C. M	D. 2, 4
<i>C. amomum</i> Mill.	B. Sh	C. M	D. 4
<i>C. asperifolia</i> Michx.			
<i>C. obliqua</i> Raf.			
<i>C. stricta</i> Lam.			
<i>C. stolonifera</i> Michx.			
<i>C. drummondii</i> Mey.			
<i>C. racemosa</i> Lam.	B. Sh	C. N	D. 4

94. *Ericaceae*

A. Genera: 12. Species: 31. B. T—1 (+2). Sh—25. (4)—5. C. MM—1.
M—11. N—12. Ch—1. H—3. G—3. D. 2—1 (+2). 3—10.
4—15. 14—1. 16—1. 17—3. 20—3.

<i>Clethra acuminata</i> Michx.	B. Sh	C. M	D. 4
<i>Chimaphila maculata</i> (L.) Pursh	B. (4)	C. Hpr	D. 16
<i>Pyrola rotundifolia</i> L.			
var. <i>americana</i> (Sweet) Fern.	B. (4)	C. Hrr	D. 14

<i>Monotropa uniflora</i> L.	B. (4)	C. Gr	D. 17, 20
<i>M. hypopithys</i> L.			
var. <i>rubra</i> (Torr.) Farw.			
<i>M. odorata</i> Ell.			
<i>Rhododendron maximum</i> L.	B. Sh, T	C. M	D. 3, 2
<i>R. catawbiense</i> Michx.	B. Sh	C. M	D. 3
<i>R. calendulaceum</i> (Michx.) Torr.			
<i>R. cumberlandense</i> Braun	B. Sh	C. N	D. 3
<i>R. nudiflorum</i> (L.) Torr.			
<i>R. roseum</i> (Loisel.) Rehd.	B. Sh	C. M	D. 3
<i>R. arborescens</i> (Pursh) Torr.	B. Sh, T	C. M	D. 3, 2
<i>Kalmia latifolia</i> L.	B. Sh	C. M	D. 3
<i>Lyonia ligustrina</i> (L.) DC.	B. Sh	C. M	D. 4
and integrating varieties			
<i>salicifolia</i> (Wats.) DC.			
<i>capreaefolia</i> (Wats.) DC.			
<i>foliosiflora</i> (Michx.) Fern.			
<i>pubescens</i> (Gray) Rehder.			
<i>Oxydendrum arboreum</i> (L.) DC.	B. T	C. MM	D. 2
<i>Epigaea repens</i> L.	B. Sh	C. Ch	D. 3
<i>Gaultheria procumbens</i> L.	B. Sh	C. Hpr	D. 3
<i>Gaylussacia brachycera</i> (Michx.) Gray	B. Sh	C. N	D. 4
<i>G. baccata</i> (Wang.) C. Koch			
<i>Vaccinium arboreum</i> Marsh.	B. Sh	C. M	D. 4
<i>V. corymbosum</i> L.	B. Sh	C. N	D. 4
<i>V. stamineum</i> L.			
<i>V. neglectum</i> (Small) Fern.			
<i>V. vacillans</i> Torr.			
<i>V. constablaei</i> Gray	B. Sh	C. M	D. 4
<i>V. simulatum</i> Small			
<i>V. pallidum</i> Ait.	B. Sh	C. N	D. 4
<i>V. alto-montanum</i> Ashe			
<i>V. missouriense</i> Ashe			
<i>V. missouriense</i> X <i>vacillans</i>			

95. *Diapensiaceae*

A. Genera: 1. Species: 1. B. (4)—1. C. G—1. D. 17—1.

Galax aphylla L. B. (4) C. Grh D. 1796. *Primulaceae*A. Genera: 4. Species: 10. B. (4)—9. (1)—1. C. Ch—1. H—8. Th—1.
D. 12—1. 14—1. 16—7. 18—1.*Samolus parviflorus* Raf. B. (4) C. Hs D. 16**Lysimachia nummularia* L. B. (4) C. Ch D. 12*L. quadrifolia* L. B. (4) C. Hpr D. 16*L. terrestris* (L.) BSP.*L. ciliata* L.*L. tonsa* Wood*L. lanceolata* Walt.*L. hybrida* Michx. B. (4) C. Hp D. 16**Anagallis arvensis* L. B. (1) C. Th D. 18*Dodecatheon meadia* L. B. (4) C. Hr D. 1497. *Sapotaceae*A. Genera: 1. Species: 1. B. T—(1). Sh—1. C. M—(1). N—1.
D. 2—(1). 4—1. 7—1.*Bumelia lycioides* (L.) Gaertn. f. B. Sh, T C. N, M
D. 4, 7, 2

98. *Ebenaceae*

- A. Genera: 1. Species: 1. B. T—1. C. MM—1. D. 2—1.
Diospyros virginiana L. B. T C. MM D. 2
 **var. *platycarpa* Sarg.
 (Gibson 106, Adair County—F)

99. *Styracaceae*

- A. Genera: 2. Species: 2. B. T—1. Sh—1. C. M—2. D. 2—1. 4—1.
Halesia carolina L. B. T C. M D. 2
Styrax americana Lam. B. Sh C. M D. 4

100. *Oleaceae*

- A. Genera: 3. Species: 7. B. T—6. Sh—1. C. MM—5. M—2. D. 2—6.
 4—1. B. T C. MM D. 2
Fraxinus americana L.
F. tomentosa Michx. f.
F. biltmoreana Beadle
F. pennsylvanica Marsh.
 var. *lanceolata* (Borkh.) Sarg.
F. quadrangulata Michx.
Chionanthus virginica L. B. T C. M D. 2
Forestiera ligustrina (Michx.) Poir. B. Sh C. M D. 4

101. *Loganiaceae*

- A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 16—1.
Spigelia marilandica L. B. (4) C. Hp D. 16

102. *Gentianaceae*

- A. Genera: 5. Species: 13. B. (4)—8 (+1). (2)—3. (1)—2. C. H—11.
 Th—2. D. 16—11. 18—2.
Sabatia angularis (L.) Pursh B. (2) C. Hs D. 16
S. stellaris Pursh B. (1) C. Th D. 18
S. campanulata (L.) Torr. B. (4) C. Hs D. 16
Bartonia paniculata (Michx.) Robins. B. (2) C. Hp D. 16
Obolaria virginica L. B. (4) C. Hp D. 16
Gentiana quinquefolia L. B. (1) C. Th D. 18
 var. *occidentalis* (Gray) Hitchc.
G. puberula Michx. B. (4) C. Hp D. 16
 ***G. andrewsii* Griseb.
 (Gibson 186 and 331,
 Adair County—F)
G. saponaria L. B. (4) C. Hpr D. 16
G. decora Pollard B. (4) C. Hp D. 16
G. flavida A. Gray
G. villosa L.
Frasera carolinensis Walt. B. (2), (4) C. Hs D. 16

103. *Apocynaceae*

- A. Genera: 4. Species: 6. B. Sh—1. (4)—5. C. M—1. Ch—1. H—4.
 D. 5—1. 12—1. 16—4.
Amsonia tabernaemontana Walt. B. (4) C. Hp D. 16
 var. *salicifolia* (Pursh) Woodson
 **Vinca minor* L. B. (4) C. Ch D. 12
Trachelospermum difforme
 (Walt.) Gray B. Sh C. M D. 5
Apocynum cannabinum L. B. (4) C. Hp D. 16
 var. *glaberrimum* A. DC.
 var. *pubescens* (Mitchell) A. DC.
A. androsaemifolium L.
A. medium Greene

104. *Asclepiadaceae*

A. Genera: 5. Species: 19. B. (4)—19. C. H—16. G—3. D. 15—1.
16—16. 17—3.

<i>Acerates hirtella</i> Pennell	B. (4)	C. Hp	D. 16
<i>A. viridiflora</i> Ell.			
<i>Asclepias tuberosa</i> L.			
<i>A. purpurascens</i> L.			
<i>A. incarnata</i> L.			
<i>A. amplexicaulis</i> J. E. Sm.			
<i>A. syriaca</i> L.	B. (4)	C. Gr	D. 17
<i>A. intermedia</i> Vail	B. (4)	C. Hp	D. 16
<i>A. sullivantii</i> Engelm.	B. (4)	C. Hs	D. 16
<i>A. phytolaccoides</i> Pursh	B. (4)	C. Hp	D. 16
<i>A. variegata</i> L.			
<i>A. quadrifolia</i> Jacq.			
<i>A. perennis</i> Walt.			
<i>A. verticillata</i> L.			
<i>Asclepiodora viridis</i> (Walt.) Gray	B. (4)	C. Grh	D. 17
<i>Ampelamus albidus</i> (Nutt.) Britt.	B. (4)	C. Gr	D. 15, 17
<i>Gonolobus gonocarpos</i> (Walt.) Perry	B. (4)	C. Hp	D. 15
<i>G. obliquus</i> (Jacq.) Schultes			
<i>G. shortii</i> Gray			

105. *Convolvulaceae*

A. Genera: 4. Species: 13. B. (4)—4. (1)—9. C. H—2. G—2. Th—9.
D. 15—1. 16—1. 17—2. 18—9. 20—5.

<i>Cuscuta pentagona</i> Engelm.	B. (1)	C. Th	D. 18, 20
<i>C. cephalanthi</i> Engelm.			
<i>C. gronovii</i> Willd.			
<i>C. compacta</i> Juss.			
<i>C. campestris</i> Yuncker			
<i>Convolvulus spithameus</i> L.	B. (4)	C. Hp	D. 16
<i>C. sepium</i> L.	B. (4)	C. Hp	D. 15
var. <i>repens</i> (L.) Gray			
<i>C. arvensis</i> L.	B. (4)	C. Gr	D. 17
* <i>Ipomoea hederacea</i> Jacq.	B. (1)	C. Th	D. 18
* <i>I. purpurea</i> (L.) Roth			
<i>I. pandurata</i> (L.) G. F. W. Mey.			
var. <i>rubescens</i> Choisy	B. (4)	C. Grt	D. 17
<i>I. lacunosa</i> L.	B. (1)	C. Th	D. 18
* <i>Quamoclit coccinea</i> (L.) Moench			

106. *Polemoniaceae*

A. Genera: 2. Species: 12. B. (4)—12. C. Ch—2. H—10. D. 9—2.
16—10.

<i>Phlox subulata</i> L.			
var. <i>australis</i> Wherry	B. (4)	C. Ch	D. 9
<i>P. bifida</i> Beck.			
var. <i>stellaria</i> (Gray) Wherry	B. (4)	C. Hpr	D. 16
<i>P. divaricata</i> L.	B. (4)	C. Ch	D. 9
<i>P. pilosa</i> L.	B. (4)	C. Hp	D. 16
<i>P. amoena</i> Sims	B. (4)	C. Hpr	D. 16
<i>P. stolonifera</i> Sims			
<i>P. carolina</i> L.			
var. <i>triflora</i> (Michx.) Wherry			
<i>P. glaberrima</i> L.	B. (4)	C. Hp	D. 16
var. <i>interior</i> Wherry			

- var. *melampyrifolia*
(Salisb.) Wherry
P. maculata L.
var. *odorata* (Sweet) Wherry
var. *pyramidalis* (Smith) Wherry
P. amplifolia Britt.
P. paniculata L.
var. *acuminata* (Pursh) Chapm.
Polemonium reptans L.
var. *villosum* Braun

107. *Hydrophyllaceae*

- A. Genera: 2. Species: 6. B. (4)—3. (2)—2. (1)—1. C. H—4. G—1.
Th—1. D. 16—4. 17—1. 18—1.

Hydrophyllum appendiculatum

Michx.	B. (2)	C. Hs	D. 16
<i>H. canadense</i> L.	B. (4)	C. Grh	D. 17
<i>H. macrophyllum</i> Nutt.	B. (4)	C. Hs	D. 16
<i>H. virginianum</i> L.	B. (4)	C. Hsr	D. 16
<i>Phacelia bipinnatifida</i> Michx.	B. (2)	C. Hp	D. 16
<i>P. purshii</i> Buckl.	B. (1)	C. Th	D. 18

108. *Boraginaceae*

- A. Genera: 9. Species: 17. B. (4)—9 (+1). (2)—5. (1)—3. C. H—14.
Th—3. D. 16—14. 18—3.

* <i>Heliotropium indicum</i> L.	B. (1)	C. Th	D. 18
<i>H. tenellum</i> (Nutt.) Torr.			
* <i>Cynoglossum officinale</i> L.	B. (2)	C. Hs	D. 16
<i>C. virginianum</i> L.	B. (4)	C. Hs	D. 16
* <i>Lappula echinata</i> Gilib.	B. (1)	C. Th	D. 18
<i>Hackelia virginiana</i> (L.)			
I. M. Johnston	B. (2)	C. Hs	D. 16
<i>Myosotis verna</i> Nutt.			
<i>M. macrosperma</i> Engelm.			
<i>Mertensia virginica</i> (L.) Link	B. (4)	C. Hs	D. 16
* <i>Lithospermum arvense</i> L.	B. (2)	C. Hs	D. 16
<i>L. latifolium</i> Michx.	B. (4)	C. Hp	D. 16
* <i>L. officinale</i> L.			
<i>L. tuberosum</i> Rugel	B. (4)	C. Hs	D. 16
<i>L. canescens</i> (Michx.) Lehm.	B. (4)	C. Hp	D. 16
** <i>L. croceum</i> Fern.			

(Gibson 289, Adair County—F.)

<i>Onosmodium hispidissimum</i> Mack.	B. (4)	C. Hs	D. 16
* <i>Echium vulgare</i> L.	B. (4), (2)	C. Hs	D. 16

109. *Verbenaceae*

A. Genera: 2. Species: 7. B. (4)—7. C. H—7. D. 16—7.			
<i>Verbena canadensis</i> (L.) Britt.	B. (4)	C. Hpr	D. 16
<i>V. urticaefolia</i> L.	B. (4)	C. Hp	D. 16
<i>V. simplex</i> Lehm.			
<i>V. hastata</i> L.			
<i>V. stricta</i> Vent.			
<i>V. bracteata</i> Lag. & Rodr.			
<i>Lippia lanceolata</i> Michx.			
var. <i>recognita</i> Fern. & Grisc.	B. (4)	C. Hpr	D. 16

110. *Labiatae*

A. Genera: 28. Species: 72. B. Sh—1. (4)—61. (2)—4. (1)—6 (+1).			
C. N—1. H—59. G—6. Th—6. D. 4—1. 16—59. 17—6. 18—6.			
<i>Teucrium canadense</i> L.	B. (4)	C. Hpr	D. 16
var. <i>virginicum</i> (L.) Eaton			
<i>T. occidentale</i> Gray			
<i>Isanthus brachiatus</i> (L.) BSP.	B. (1)	C. Th	D. 18
<i>Trichostema dichotomum</i> L.			
<i>Scutellaria nervosa</i> Pursh	B. (4)	C. Hpr	D. 16
<i>S. ambigua</i> Nutt.	B. (4)	C. Gst	D. 17
<i>S. leonardi</i> Epl.			
<i>S. parvula</i> Michx.			
var. <i>australis</i> (Fassett) Epl.			
<i>S. laterifolia</i> L.	B. (4)	C. Hpr	D. 16
<i>S. saxatilis</i> Riddell			
<i>S. ovata</i> Hill			
ssp. <i>calcareae</i> Epl.			
ssp. <i>pseudovenosa</i> Epl.			
<i>S. incana</i> Spreng.	B. (4)	C. Hp	D. 16
<i>S. punctata</i> Leon			
<i>S. serrata</i> Andr.			
<i>S. ovalifolia</i> Pers.	B. (4)	C. Hpr	D. 16
ssp. <i>mollis</i> Epl.			
ssp. <i>hirsuta</i> (Short) Epl.			
<i>S. integrifolia</i> L.			
* <i>Marrubium vulgare</i> L.	B. (4)	C. Hp	D. 16
<i>Agastache nepetoides</i> (L.) Ktze.	B. (4)	C. Hs	D. 16
<i>A. scrophulariaefolia</i> (Willd.) Ktze.			
<i>Meehania cordata</i> (Nutt.) Britt.	B. (4)	C. Hpr	D. 16
* <i>Nepeta cataria</i> L.	B. (4)	C. Hp	D. 16
* <i>Glecoma hederacea</i> L.	B. (4)	C. Hpr	D. 16
var. <i>parviflora</i> (Benth.) House			
* <i>Prunella vulgaris</i> L.	B. (4)	C. Hsr	D. 16
var. <i>lanceolata</i> (Bart.) Fern.			
<i>Physostegia denticulata</i> (Ait.) Britt.	B. (4)	C. Hp	D. 16
<i>P. virginiana</i> (L.) Benth.			
<i>P. speciosa</i> (Sweet) Sweet			
<i>Synandra hispidula</i> (Michx.) Britt.	B. (2)	C. Hp	D. 16
* <i>Lamium amplexicaule</i> L.	B. (2), (1)	C. Hp	D. 16
* <i>L. purpureum</i> L.	B. (1)	C. Th	D. 18
* <i>L. cordiaca</i> L.	B. (4)	C. Hp	D. 16
* <i>L. marrubiastrum</i> L.	B. (2)	C. Hp	D. 16
* <i>L. sibiricus</i> L.			
<i>Stachys tenuifolia</i> Willd.	B. (4)	C. Hpr	D. 16
<i>S. nuttallii</i> Shuttlw.	B. (4)	C. Gst	D. 17
<i>S. palustris</i> L.			
var. <i>homotricha</i> Fern.			
<i>S. riddellii</i> House	B. (4)	C. Hpr	D. 16
<i>Salvia urticifolia</i> L.	B. (4)	C. Hs	D. 16
<i>S. lyrata</i> L.			
<i>S. azurea</i> Lam.			
var. <i>grandiflora</i> Benth.			
* <i>S. sylvestris</i> L.	B. (4)	C. Hsr	D. 16
<i>Monarda didyma</i> L.	B. (4)	C. Hpr	D. 16
<i>M. bradburiana</i> Beck			

<i>M. clinipodia</i> L.				
<i>M. fistulosa</i> L.				
var. <i>mollis</i> (L.) Benth.				
<i>Blephilia ciliata</i> (L.) Raf.				
<i>B. hirsuta</i> (Pursh) Benth.				
<i>Hedeoma pulegioides</i> (L.) Pers.	B. (1)	C. Th	D. 18	
* <i>Melissa officinalis</i> L.	B. (4)	C. Hpr	D. 16	
* <i>Satureja nepeta</i> (L.) Scheele				
<i>S. glabella</i> (Michx.) Briq.	B. (4)	C. Hp	D. 16	
<i>S. vulgaris</i> (L.) Fritsch	B. (4)	C. Hpr	D. 16	
<i>Conradina verticillata</i> Jennison	B. Sh	C. N	D. 4	
<i>Pycnanthemum flexuosum</i> (Walt.) BSP.	B. (4)	C. Hpr	D. 16	
<i>P. virginianum</i> (L.) Durand & Jackson				
<i>P. pilosum</i> Nutt.				
<i>P. verticillatum</i> (Michx.) Pers.				
<i>P. albescens</i> T. & G.				
<i>P. incanum</i> (L.) Michx.				
<i>P. pycnanthemoides</i> (Leavenw.) Fern.				
<i>Cunila origanoides</i> (L.) Britt.	B. (4)	C. Hp	D. 16	
<i>Lycopus rubellus</i> Moench	B. (4)	C. Hpr	D. 16	
<i>L. americanus</i> Muhl.				
<i>L. uniflorus</i> Michx.				
<i>L. virginicus</i> L.				
* <i>Mentha longifolia</i> (L.) Huds. var. <i>mollissima</i> (Borkh.) Rouy (Meade County — Davies, 1955. Univ. Louisville herbarium.)				
* <i>M. spicata</i> L.				
* <i>M. piperita</i> L.				
* <i>M. citrata</i> Ehrh.				
* <i>M. arvensis</i> L. var. <i>canadensis</i> (L.) Briq.				
<i>Collinsonia canadensis</i> L.	B. (4)	C. Gst	D. 17	
* <i>Perilla frutescens</i> (L.) Britt.	B. (1)	C. Th	D. 18	
** <i>Mosla dianthera</i> (Hamilton) Maxim. (Braun 4874, McCreary County — F)				

111. *Solanaceae*

A. Genera: 5. Species: 12. B. Sh—2. (4)—5. (1)—5. C. M—1. N—1. G—5. Th—5. D. 5—2. 7—2. 17—5. 18—5.				
* <i>Nicandra physalodes</i> (L.) Pers.	B. (1)	C. Th	D. 18	
* <i>Lycium halimifolium</i> Mill.	B. Sh	C. M	D. 5	
<i>Physalis subglabrata</i> Mack. & Bush	B. (4)	C. Grh	D. 17	
<i>P. virginiana</i> Mill.				
<i>P. pubescens</i> L.	B. (1)	C. Th	D. 18	
<i>P. heterophylla</i> Nees	B. (4)	C. Grh	D. 17	
<i>P. ambigua</i> (Gray) Rydb.				
<i>Solanum carolinense</i> L.	B. (4)	C. Gr	D. 7, 17	
<i>S. rostratum</i> Dunal	B. (1)	C. Th	D. 7, 18	
<i>S. nigrum</i> L.	B. (1)	C. Th	D. 18	
<i>S. dulcamara</i> L.	B. Sh	C. N	D. 5	

**Datura stramonium* L. B. (1) C. Th D. 18

112. *Scrophulariaceae*

A. Genera: 23. Species: 55. B. (4)—32. (2)—6. (1)—17 (+2).
C. Ch—5. H—32. G—1. Th—17. D. 12—5. 16—32. 17—1.

18—17. 20—1.

Hydrantheum rotundifolium B. (4) C. Ch D. 12

(Michx.) Pennell

Gratiola neglecta Torr. B. (1) C. Th D. 18

G. lutea Raf.

(Harlan County — Barbour
and Barbour. 1950. CU)

G. virginiana L.

Tragiola pilosa (Michx.)

Small & Pennell

B. (4) C. Hs D. 16

Leucospora multifida (Michx.) Nutt.

B. (1) C. Th D. 18

Mimulus ringens L.

B. (4) C. Hpr D. 16

M. alatus Ait.

Lindernia dubia (L.) Pennell

var. *major* (Pursh) Pennell

B. (1) C. Th D. 18

L. anagallidea (Michx.) Pennell

**Verbascum blattaria* L.

B. (2) C. Hs D. 16

**V. thapsus* L.

**V. phlomoides* L.

Chelone glabra L.

B. (4) C. Hpr D. 16

var. *elatior* Raf.

C. obliqua L.

var. *speciosa* Pennell & Wherry

Penstemon digitalis Nutt.

B. (4) C. Hs D. 16

P. alluviorum Pennell

P. calycosus Small

P. laevigatus Ait.

P. canescens Britt.

P. pallidus Small

P. brevisepalus Pennell

P. tenuiflorus Pennell

P. hirsutus (L.) Willd.

Scrophularia marilandica L.

B. (4) C. Hp D. 16

Collinsia verna Nutt.

B. (2) C. Hp D. 16

**Linaria vulgaris* Hill

B. (4) C. Hpr D. 16

**Kickxia elatine* (L.) Dumort.

B. (1) C. Th D. 18

Veronicastrum virginicum (L.) Farw.

B. (4) C. Grh D. 17

**Veronica serpyllifolia* L.

B. (4) C. Hp D. 16

V. peregrina L.

B. (1) C. Th D. 18

**V. arvensis* L.

**V. officinalis* L.

B. (4) C. Ch D. 12

V. americana (Raf.) Schwein.

V. glandifera Pennell

V. comosa Richter

**V. persica* Poir.

B. (1) C. Ch D. 18

Aureolaria virginica (L.) Pennell

B. (4) C. Hp D. 16

A. laevigata (Raf.) Raf.

A. flava (L.) Farw.

var. *macrantha* Pennell

A. patula (Chapm.) Pennell

- A. pedicularis* (L.) Raf.
 var. *austromontana* Pennell B. (2), (1) C. Hp D. 16
A. pectinata (Nutt.) Pennell B. (1) C. Th D. 18
 var. *eurycarpa* Pennell B. (4) C. Hp D. 16
Dasistoma macrophylla (Nutt.) Raf. B. (1) C. Th D. 18
Gerardia purpurea L. B. (4) C. Hpr D. 16
G. tenuifolia Vahl B. (4) C. Hp D. 16
 var. *macrophylla* Benth.
G. skinneriana Wood
G. decemloba Greene
G. gattingeri Small
Buchnera americana L. B. (4) C. Hpr D. 16
Schwalbea australis Pennell B. (4) C. Hp D. 16
Pedicularis lanceolata Michx. B. (4) C. Hs D. 16
P. canadensis L.
Castilleja coccinea (L.) Spreng. B. (2), (1) C. Hs
 D. 16, 20
Melampyrum lineare Lam.
 var. *pectinatum* Pennell B. (1) C. Th D. 18
 113. *Bignoniaceae*
 A. Genera: 4. Species: 4. B. T—2. Sh—2. C. MM—4. D. 2—2. 5—2.
Bignonia capreolata L. B. Sh C. MM D. 5
Campsis radicans (L.) Seem.
Catalpa speciosa Warder B. T C. MM D. 2
 **Paulownia tomentosa*
 (Thunb.) Steud.
 114. *Martyniaceae*
 A. Genera: 1. Species: 1. B. (1)—1. C. Th—1. D. 18—1.
Proboscidea louisianica (Mill.) Thell. B. (1) C. Th D. 18
 115. *Orobanchaceae*
 A. Genera: 3. Species: 4. B. (4)—4. C. G—4. D. 17—4. 20—4.
Conopholis americana (L.f.) Wallr. B. (4) C. Gp D. 17, 20
Orobanche ludoviciana Nutt.
O. uniflora L.
Epifagus virginiana (L.) Bart.
 116. *Lentibulariaceae*
 A. Genera: 1. Species: 1. B. (4)—1. C. HH—1. D. 19—1.
Utricularia gibba L. B. (4) C. HH D. 19
 117. *Acanthaceae*
 A. Genera: 2. Species: 4. B. (4)—4. C. G—3. HH—1. D. 16—1. 17—4.
Ruellia caroliniensis (Walt.) Steud. B. (4) C. Grh D. 17
 var. *parviflora* (Nees) Blake
R. strepens L.
R. pedunculata Torr. B. (4) C. HH D. 16
Justicia americana (L.) Vahl
 118. *Phrymaceae*
 A. Genera: 1. Species: 1. B. (4)—1. C. H—1. D. 16—1.
Phryma leptostachya L. B. (4) C. Hp D. 16
 119. *Plantaginaceae*
 A. Genera: 1. Species: 5. B. (4)—2. (2)—1 (+1). (1)—2 (+1).
 C. H—3. Th—2 (+1). D. 14—3. 18—2 (+1).
Plantago rugellii Dcne. B. (4) C. Hr D. 14
 var. *asperula* Farw.
 **P. lanceolata* L. B. (4), (2) C. Hr D. 14
 var. *sphaerostachya* Mert. & Koch

<i>P. aristata</i> Michx.	B. (1)	C. Th	D. 18
<i>P. virginica</i> L.	B. (2), (1)	C. Hr, Th	
	D. 14, 18		
<i>P. pusilla</i> Nutt.	B. (1)	C. Th	D. 18

120. *Rubiaceae*

A. Genera: 6. Species: 24. B. Sh—1. (4)—21. (1)—2. C. M—1. Ch —1. H—20. Th—2. D. 4—1. 12—1. 16—20. 18—2.			
<i>Houstonia caerulea</i> L.	B. (4)	C. Hsr	D. 16
<i>H. serpyllifolia</i> Michx.			
<i>H. purpurea</i> L.			
var. <i>pubescens</i> Britt.	B. (4)	C. Hs	D. 16
<i>H. longifolia</i> Gaertn.			
<i>H. lanceolata</i> (Poir.) Britt.			
<i>H. tenuifolia</i> Nutt.			
<i>H. canadensis</i> Willd.			
<i>H. nigricans</i> (Lam.) Fern.			
<i>Cephalanthus occidentalis</i> L.			
var. <i>pubescens</i> Raf.	B. Sh	C. M	D. 4
<i>Mitchella repens</i> L.	B. (4)	C. Ch	D. 12
<i>Diodia teres</i> Walt.			
var. <i>setifera</i> Fern. & Grisc.	B. (1)	C. Th	D. 18
<i>D. virginiana</i> L.	B. (4)	C. Hp	D. 16
<i>Spermacoce glabra</i> Michx.			
<i>Galium aparine</i> L.	B. (1)	C. Th	D. 18
<i>G. pilosum</i> Ait.	B. (4)	C. Hp	D. 16
var. <i>puncticulosum</i> (Michx.) T. & G.			
<i>G. circaeans</i> Michx.			
var. <i>hypomalacum</i> Fern.	B. (4)	C. Hpr	D. 16
<i>G. lanceolatum</i> Torr.	B. (4)	C. Hp	D. 16
<i>G. latifolium</i> Michx.			
<i>G. obtusum</i> Bigel.			
<i>G. tinctorium</i> L.	B. (4)	C. Hpr	D. 16
* <i>G. pedemontanum</i> All.	B. (4)	C. Hp	D. 16
<i>G. concinnum</i> T. & G.			
<i>G. triflorum</i> Michx.			
<i>G. trifidum</i> L.			
ssp. <i>tinctorium</i> (L.) Fern.			

121. *Caprifoliaceae*

A. Genera: 5. Species: 21. B. Sh—18. (4)—3. C. M—14. N—4. H—3. D. 4—18. 16—3.			
<i>Sambucus canadensis</i> L.	B. Sh	C. M	D. 4
<i>S. pubens</i> Michx.			
<i>Viburnum acerifolium</i> L.			
<i>V. recognitum</i> Fern.			
<i>V. dentatum</i> L.			
var. <i>deamii</i> (Rehder) Fern.			
var. <i>pubescens</i> (Ait.) Pursh			
<i>V. molle</i> Michx.			
<i>V. rafinesquianum</i> Schultes	B. Sh	C. N	D. 4
<i>V. affine</i> Bush			
var. <i>hypomalacum</i> Blake			
<i>V. cassinoides</i> L.	B. Sh	C. M	D. 4
<i>V. lentago</i> L.			
<i>V. prunifolium</i> L.			

V. rufidulum Raf.*Triosteum perfoliatum* L. B. (4) C. Hp D. 16*T. aurantiacum* Bickn.var. *glaucescens* Wieg.*T. angustifolium* L.*Symphoricarpos orbiculatus* Moench B. Sh C. N D. 4**Lonicera japonica* Thunb. B. Sh C. M D. 4*L. dioica* L.*L. glaucescens* Rydb.*L. prolifera* (Kirchner) Rehd.*L. sempervirens* L.122. *Valerianaceae*A. Genera: 2. Species: 2. B. (4)—1. (1)—1. C. H—1. Th—1.
D. 16—1. 18—1.*Valerianella intermedia* Dyal B. (1) C. Th D. 18*Valeriana pauciflora* Michx. B. (4) C. Hsr D. 16123. *Dipsacaceae*

A. Genera: 1. Species: 1. B. (2)—1. C. H—1. D. 16—1.

**Dipsacus sylvestris* Huds. B. (2) C. Hs D. 16124. *Cucurbitaceae*A. Genera: 4. Species: 4. B. (4)—2. (1)—2. C. H—2. Th—2. D. 15—2.
18—2.*Melothria pendula* L. B. (4) C. Hp D. 15*Cucurbita foetidissima* HBK.*Echinocystis lobata* (Michx.) T. & G. B. (1) C. Th D. 18*Sicyos angulatus* L.125. *Campanulaceae*A. Genera: 2. Species: 3. B. (4)—1. (2)—1. (1)—1. C. H—2. Th—1.
D. 16—2. 18—1.*Campanula americana* L. B. (2) C. Hp D. 16*C. divaricata* Michx. B. (4) C. Hpr D. 16*Specularia perfoliata* (L.) A. DC. B. (1) C. Th D. 18126. *Lobeliaceae*

A. Genera: 1. Species: 7. B. (4)—5. (2)—2. C. H—7. D. 16—7.

Lobelia cardinalis L. B. (4) C. Hs D. 16*L. siphilitica* L.*L. amoena* Michx.*L. puberula* Michx.*L. nuttallii* R. & S.*L. inflata* L. B. (2) C. Hs D. 16*L. spicata* Lam.var. *originalis* McVaughvar. *leptostachys* (A. DC.)

Mack. & Bush

127. *Compositae*A. Genera: 61. Species: 248. B. (4)—190 (+1). (2)—17 (+3).
(1)—41 (+6). C. Ch—5. H—185. G—17. Th—41. D. 7—10.
12—5. 14—5. 16—181. 17—17. 18—41.*Vernonia noveboracensis* (L.) Michx. B. (4) C. Hp D. 16*V. fasciculata* Michx.*V. altissima* Nutt.*V. missurica* Raf.*Elephantopus carolinianus* Willd.*E. tomentosus* L.

<i>S. arguta</i> Ait.			
<i>S. harrisii</i> Steele	B. (4)	C. Hsr	D. 16
<i>S. patula</i> Muhl.	B. (4)	C. Hs	D. 16
** <i>S. strigosa</i> Small (Gibson 168, Adair County — F)			
<i>S. nemoralis</i> Ait.			
<i>S. caesia</i> L.	B. (4)	C. Hpr	D. 16
<i>S. latifolia</i> L.			
<i>S. albopilosa</i> Braun			
<i>S. curtisii</i> T. & G.			
var. <i>pubens</i> (M. A. Curtis) Gray			
<i>S. rugosa</i> Mill.			
var. <i>aspera</i> Ait.			
<i>S. gigantea</i> Ait.			
var. <i>leiophylla</i> (Ait.) Fern.			
<i>S. canadensis</i> L.			
var. <i>gilvocanescens</i> Rydb.			
<i>S. altissima</i> L.	B. (4)	C. Hsr	D. 16
<i>S. shortii</i> T. & G.	B. (4)	C. Hp	D. 16
<i>S. graminifolia</i> (L.) Salisb.			
var. <i>nuttallii</i> (Greene) Fern.			
<i>S. rigida</i> L.			
var. <i>glabrata</i> Braun	B. (4)	C. Hs	D. 16
<i>S. sphacelata</i> Raf.			
<i>Astranthium integrifolium</i>	B. (1)	C. Th	D. 18
(Michx.) Nutt.			
* <i>Bellis perennis</i> L.	B. (4)	C. Hr	D. 14
<i>Boltonia interior</i> (Fern. & Grisc.)	B. (4)	C. Hpr	D. 16
G. N. Jones			
<i>B. latisquama</i> Gray			
var. <i>recognita</i> Fern. & Grisc.			
<i>Aster divaricatus</i> L.	B. (4)	C. Hsr	D. 16
<i>A. macrophyllus</i> L.			
var. <i>ianthus</i> (Burgess) Fern.			
var. <i>velutinus</i> Burgess			
<i>A. schreberi</i> Nees			
<i>A. shortii</i> Lindl.	B. (4)	C. Hs	D. 16
<i>A. camptosorus</i> Small			
<i>A. cordifolius</i> L.	B. (4)	C. Hsr	D. 16
<i>A. lowrieanus</i> Porter			
<i>A. sagittifolius</i> Wedemeyer	B. (4)	C. Hs	D. 16
<i>A. drummondii</i> Lindl.			
<i>A. undulatus</i> L.	B. (4)	C. Hsr	D. 16
<i>A. puniceus</i> L.	B. (4)	C. Hpr	D. 16
<i>A. laevis</i> L.	B. (4)	C. Hs	D. 16
var. <i>falcatus</i> Farw.			
<i>A. laevis</i> X <i>cordifolius</i>			
<i>A. patens</i> Ait.	B. (4)	C. Hpr	D. 16
var. <i>gracilis</i> Hook.			
var. <i>phlogifolius</i> Nees			
<i>A. oblongifolius</i> Nutt.	B. (4)	C. Hsr	D. 16
<i>A. novae-angliae</i> L.	B. (4)	C. Hpr	D. 16
<i>A. prenanthoides</i> Muhl.	B. (4)	C. Hsr	D. 16
<i>A. concolor</i> L.	B. (4)	C. Hp	D. 16
<i>A. sericeus</i> Vent.	B. (4)	C. Hs	D. 16

<i>A. surculosus</i> Michx.	B. (4)	C. Hpr	D. 16
<i>A. dumosus</i> L.			
var. <i>coridifolius</i> (Michx.) T. & G.	B. (4)	C. Hs	D. 16
<i>A. vimineus</i> Lam.			
var. <i>subdumosus</i> Wieg.	B. (4)	C. Hsr	D. 16
<i>A. lateriflorus</i> (L.) Britt.			
var. <i>angustifolius</i> Wieg.			
var. <i>pendulus</i> (Ait.) Burgess			
<i>A. pantotrichus</i> Blake			
<i>A. paniculatus</i> Lam.			
var. <i>simplex</i> (Willd.) Burgess			
<i>A. pilosus</i> Willd.	B. (4)	C. Hs	D. 16
var. <i>demotus</i> Blake			
var. <i>platyphyllus</i> (T. & G.) Blake			
<i>A. umbellatus</i> Mill.	B. (4)	C. Hpr	D. 16
<i>A. infirmus</i> Michx.			
<i>A. linariifolius</i> L.			
<i>Erigeron pulchellus</i> Michx.	B. (4)	C. Hsr	D. 16
var. <i>braunii</i> Fern.			
<i>E. philadelphicus</i> L.			
<i>E. ramosus</i> (Walt.) BSP.	B. (1)	C. Th	D. 18
<i>E. annuus</i> (L.) Pers.			
<i>E. canadensis</i> L.			
<i>E. pusillus</i> Nutt.			
<i>E. divaricatus</i> Michx.			
<i>Seriocarpus asteroides</i> (L.) BSP.	B. (4)	C. Hs	D. 16
<i>S. linifolius</i> (L.) BSP.			
<i>Pluchea camphorata</i> (L.) DC.	B. (1)	C. Th	D. 18
<i>Antennaria parlinii</i> Fern.	B. (4)	C. Ch	D. 12
<i>A. plantaginifolia</i> (L.) Richards			
<i>A. fallax</i> Greene			
var. <i>calophylla</i> (Greene) Fern.			
<i>A. neglecta</i> Greene			
<i>A. solitaria</i> Rydb.			
<i>Gnaphalium obtusifolium</i> L.	B. (1)	C. Th	D. 18
var. <i>micradenium</i> Weath.			
<i>G. uliginosum</i> L.			
<i>G. purpureum</i> L.	B. (2), (1) D. 16 (18)	C. Hsr	
<i>Polymnia canadensis</i> L.	B. (4)	C. Hp	D. 16
<i>P. uvedalia</i> L.			
<i>Silphium laciniatum</i> L.			
var. <i>robinsonii</i> Perry	B. (4)	C. Hs	D. 16
<i>S. terebinthinaceum</i> Jacq.			
var. <i>pinnatifidum</i> (Ell.) Gray			
<i>S. trifoliatum</i> L.	B. (4)	C. Hp	D. 16
<i>S. incisum</i> Greene			
<i>S. integrifolium</i> Michx.	B. (4)	C. Hpr	D. 16
<i>S. perfoliatum</i> L.	B. (4)	C. Hs	D. 16
<i>Parthenium integrifolium</i> L.	B. (4)	C. Hpr	D. 16
<i>Iva ciliata</i> Willd.	B. (1)	C. Th	D. 18
<i>Ambrosia bidentata</i> Michx.			

<i>A. trifida</i> L.				
var. <i>integrifolia</i> (Muhl.) T. & G.				
(Ballard County — Anderson, 1947. IA)				
<i>A. elatior</i> L.				
<i>Xanthium chinense</i> Mill.				
<i>X. pennsylvanicum</i> Wallr.				
<i>X. italicum</i> Moretti				
* <i>X. spinosum</i> L.	B. (1)	C. Th	D. 7, 18	
<i>Heliopsis helianthoides</i> (L.) Sweet	B. (4)	C. Grh	D. 17	
var. <i>scabra</i> (Dunal) Fern.				
<i>Eclipta alba</i> (L.) Hassk.	B. (1)	C. Th	D. 18	
<i>Rudbeckia laciniata</i> L.	B. (4)	C. Hs	D. 16	
<i>R. umbrosa</i> Boynton & Beadle				
<i>R. fulgida</i> Ait.				
<i>R. truncata</i> Small	B. (4)	C. Hsr	D. 16	
<i>R. tenax</i> C. L. Boynt. & Beadle				
<i>R. triloba</i> L.	B. (4)	C. Hs	D. 16	
<i>R. pinnatifida</i> (T. & G.) Beadle				
<i>R. hirta</i> L.	B. (2), (1)	C. Hs		
var. <i>monticola</i> (Small) Fern.	D. 16 (18)			
<i>Brauneria purpurea</i> (DC.) Britt.	B. (4)	C. Hs	D. 16	
<i>B. pallida</i> (Nutt.) Britt.				
<i>Ratibida pinnata</i> (Vent.) Barnh.				
<i>Helianthus angustifolius</i> L.	B. (4)	C. Hsr	D. 16	
<i>H. atrorubens</i> L.	B. (4)	C. Hs	D. 16	
var. <i>pubescens</i> Ktze.				
<i>H. annuus</i> L.	B. (1)	C. Th	D. 18	
<i>H. occidentalis</i> Riddell	B. (4)	C. Hsr	D. 16	
<i>H. dowellianus</i> M. A. Curtis	B. (4)	C. Hs	D. 16	
<i>H. glaucus</i> Small	B. (4)	C. Hp	D. 16	
<i>H. microcephalus</i> T. & G.				
<i>H. decapetalus</i> L.	B. (4)	C. Grh	D. 17	
<i>H. mollis</i> Lam.				
<i>H. divaricatus</i> L.				
<i>H. hirsutus</i> Raf.				
<i>H. maximiliani</i> Schrad.				
<i>H. grosseserratus</i> Martens				
<i>H. giganteus</i> L.	B. (4)	C. Hp	D. 16	
<i>H. tuberosus</i> L.	B. (4)	C. Gst	D. 17	
<i>H. strumosus</i> L.	B. (4)	C. Grh	D. 17	
<i>Actinomeris alternifolia</i> (L.) DC.	B. (4)	C. Hp	D. 16	
<i>Verbesina helianthoides</i> Michx.				
<i>V. occidentalis</i> (L.) Walt.				
<i>V. virginica</i> L.				
<i>Coreopsis lanceolata</i> L.	B. (4)	C. Hsr	D. 16	
var. <i>villosa</i> Michx.				
<i>C. auriculata</i> L.				
<i>C. major</i> Walt.				
var. <i>stellata</i> (Nutt.) Robins.				
<i>C. pubescens</i> Ell.	B. (4)	C. Hs	D. 16	
var. <i>robusta</i> A. Gray ex Eames.				
<i>C. tripteris</i> L.				
var. <i>deamii</i> Standl.				
var. <i>intercedens</i> Standl.				

***C. verticillata* L.(Philip Albion, Jefferson
County — KY)*Bidens aristosa* (Michx.) Britt. B. (1) C. Th D. 18
var. *fritcheyi* Fern.var. *mutica* Gray ex Gattinger.*B. polylepis* Blake*B. coronata* (L.) Britt.var. *tenuiloba* (Gray) Sherff*B. frondosa* L.*B. vulgata* Greene*B. comosa* (Gray) Wieg.*B. connata* Muhl.var. *petiolata* (Nutt.) Farw.*B. cernua* L.*B. bipinnata* L.**Galinsoga ciliata* (Raf.) Blake*Marshallia grandiflora*

B. (4) C. Hs D. 16

C. L. Boynt. & Beadle

Helenium tenuifolium Nutt.

B. (1) C. Th D. 18

H. autumnale L.

B. (4) C. Hs D. 16

H. nudiflorum Nutt.*Dyssodia papposa* (Vent.) Hitchc.

B. (1) C. Th D. 18

**Anthemis cotula* L.*Achillea millefolium* L.

B. (4) C. Hsr D. 16

**Matricaria inodora* L.

B. (1) C. Th D. 18

**Chrysanthemum leucanthemum* L.

B. (4) C. Hs D. 16

var. *pinnatifidum* Lecoq.

& Lamotte

C. parthenium* (L.) Pers.Tanacetum vulgare* L.*Artemisia biennis* Willd.B. (2), (1) C. Hs
D. 16 (18)**A. annua* L.

B. (1) C. Th D. 18

**A. vulgaris* L.

B. (4) C. Hs D. 16

Erechtites hieracifolia (L.) Raf.

B. (1) C. Th D. 18

Cacalia suaveolens L.

B. (4) C. Hs D. 16

C. atriplicifolia L.*C. muehlenbergii* (Sch. Bip.) Fern.*Senecio glabellus* Poir.

B. (1) C. Th D. 18

S. aureus L.

B. (4) C. Hs D. 16

S. obovatus Muhl.

B. (4) C. Hsr D. 16

var. *rotundus* Britt.*S. pauperculus* Michx.

B. (4) C. Hs D. 16

S. plattensis Nutt.

B. (4) C. Hsr D. 16

S. smallii Britt.

B. (4) C. Hs D. 16

Arctium minus (Hill) Bernh.

B. (2) C. Hs D. 16

***A. tomentosum* Hill.

(Gibson 166, Adair County — F)

Cirsium muticum Michx.

B. (2) C. Hs D. 7, 16

C. vulgare (Savi) Tenore

(Meade County — Davies.

University of Louisville)

C. virginianum (L.) Michx.*C. altissimum* (L.) Spreng.

<i>C. discolor</i> (Muhl.) Spreng.				
* <i>C. arvense</i> (L.) Scop.	B. (4)	C. Gr	D. 7, 17	
* <i>Onopordum acanthium</i> L.	B. (2)	C. Hs	D. 7, 16	
* <i>Centaurea maculosa</i> Lam.	B. (2)	C. Hs	D. 16	
<i>Serinia oppositifolia</i> (Raf.) Ktze.	B. (1)	C. Th	D. 18	
* <i>Cichorium intybus</i> L.	B. (4)	C. Hs	D. 16	
<i>Krigia virginica</i> (L.) Willd.	B. (1)	C. Th	D. 18	
<i>K. dandelion</i> (L.) Nutt.	B. (4)	C. Hrr	D. 14	
<i>K. biflora</i> (Walt.) Blake	B. (4)	C. Hs	D. 16	
* <i>Tragopogon porrifolius</i> L.	B. (4), (2)	C. Hs	D. 16	

TABLE VI.—Summary of introduced species

[illegible]

**Taraxacum palustre* (Lyons)

Lam. & DC.

var. *vulgare* (Lam.) Fern.

B. (4) C. Hr D. 14

T. laevigatum (Willd.) DC.*T. officinale* Weber

(Meade County — Davies, 1955.

University of Louisville)

**Sonchus oleraceus* L.

B. (1) C. Th D. 18

**S. asper* (L.) Hill.

B. (1) C. Th D. 7, 18

**Lactuca scariola* L.

B. (2), (1) C. Hs

var. *integrata* Gren. & Godr.

D. 16 (18)

**L. saligna* L.

B. (2) C. Hs D. 16

L. canadensis L.

B. (2), (1) C. Hs D. 16

var. *integrifolia* (Bigel.) Grayvar. *latifolia* O. Ktze.var. *obovata* Wieg.*L. villosa* Jacq.

B. (1) C. Th D. 18

L. floridana (L.) Gaertn.

B. (2) C. Hs D. 16

L. biennis (Moench) Fern.*Pyrrhopappus carolinianus*

B. (2), (1) C. Hs

(Walt.) DC.

D. 16 (18)

**Crepis pulchra* L.

B. (1) C. Th D. 18

Prenanthes altissima L.

B. (4) C. Hsr D. 16

P. alba L.

B. (4) C. Hs D. 16

P. serpentaria Pursh*P. trifoliata* (Cass.) Fern.*P. cylindrica* (Small) Braun***P. crepidinea* Michx.

(D. V. Terrill,

Fayette County — KY)

P. aspera Michx.*Hieracium paniculatum* L.*H. scabrum* Michx.*H. gronovii* L.*H. longipilum* Torr.

B. (4) C. Hs D. 7, 16

H. venosum L.

B. (4) C. Hs D. 16

H. greenii Porter & Britt.

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Ecology of Some Earthworms With Special Reference to Seasonal Activity

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ABSTRACT: Earthworm activity is limited, rather generally, to certain seasons: in the monsoon tropical climate of Burma and in the humid subtropical climate of India, to 4-6 months of the rainy season, *i.e.*, some portion of May-October; in the humid continental climate of central Maine, to spring and fall months. Breeding, rather generally, is limited in India-Burma to a short period at end of the rainy season but in Maine to early spring and late fall. Exceptions, in each area, include limicolous species and individuals of other species in permanently moist sites. Some oriental species do not take advantage of artificially supplied moisture and become quiescent before end of the rainy season. Inactivity in India and Burma extends through hot and cold seasons. Peregrine species are more likely to remain active in exceptional sites and artificial conditions.

INTRODUCTION

Studies of the earthworm fauna of four areas, three prematurely ended and the other unlikely to be completed, provided the data that enabled the present contribution. The section on oriental species is from a manuscript written during tenure of a Guggenheim Fellowship. Most of the collecting in Maine was done by the writer for recreation and exercise during that Fellowship, while engaged in research financed by the Rockefeller Foundation and subsequently by the National Science Foundation or previously while teaching at Waterville. Several individuals have assisted in the collecting but especial thanks are due to Gerald Kinney for various interesting and important lots which otherwise would not have been secured.

RANGOON, BURMA

One sample of the data secured is presented in Table I. The species listed therein are the larger ones, but to them belonged a major portion of the 6000-odd earthworms secured during the academic year, June-March 1932-1933, in a sector of the Rangoon municipality centering at the biology building of Judson College. Collections were made by a laboratory steward in such hours as were free from more urgent duties. Each sort of habitat within the area was checked several times a month. Except on rare occasions, and then mostly after heavy rain, earthworms could be obtained only by digging.

The earthworm year in Rangoon usually begins, appropriately enough, in the same month as the academic year. All but two of the larger Rangoon species were represented in collections secured during June 1932. The absence of at least one species is noteworthy, as *Pheretima anomala* was not obtained in 1929-1933 until July —

TABLE I.—Numbers and stages of larger earthworm species collected in the Koke Quarter of Rangoon during 1932-1933¹

	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
<i>Plutellus</i>	7-0-2 ²	-13-20	-51-	-7-						
<i>Drawida</i>	2-	6-	1-	-9-						
	3-	27-	4-	3-			1-	7-	2-	1-
	16-	73-8-	29-0-21	39-0-23	1-0-3	-11	2-0-11 ³	1-	38-0-26 ³	59-0-48 ³
	64-	72-1-	18-	49-0-19	1-	-2	-2	4-0-2		2-
	2-	6-	5-3-	-9-	-5			1-		
	70-	48-	-9	-13-10	144-0-12	9-0-1	2-	1-		
<i>Lampito</i>	45-0-4	1-0-26	1-0-21	3-0-1	14-0-4	18-0-6	6-0-5	8-0-6	6-0-10	9-0-21
<i>Pheretima</i>	2-	1-	3-0-7	-1	-7					
		19-	-37	-10	-38	-1				
	2-	26-	14-0-6	2-19-137	-220	-14	-11	-1		
	2-									
	6-	23-18-12	14-0-24	3-7-23	-81	-18	-6	-6		
	38-3-	70-16-46	7-0-67	-63	-220	-13	-19	-6	-6	
	2-	1-	24-	3-	-6	-10	-1	-1		
	2-	86-3-18	16-0-29	9-0-16	2-0-34	-10	-12	1-0-14	-4	-3
<i>Perionyx</i>	40-0-15	10-10-14	23-0-16	-7	20-	9-	9-0-7	16-0-5	17-0-12	40-0-42
<i>Octochaetoides</i>	161-5-1	111-7-5	36-0-37	24-0-72	7-0-7	4-0-94	-39	7-0-161	27-0-161	5-0-55
<i>Eutyphoeus</i>	159-	54-12-44	46-0-45	26-0-73	-22	-1				
	82-	22-2-	3-0-3	11-0-11	9-0-19					
		14-0-6	-6	-12						
<i>Pontoscolex</i>	14-	-15	-5	-11	-51	-16	2-0-29	-29	3-0-16	8-0-9
<i>Glyphidrilus</i>	8-	5-	3-	2-	5-			10-	11-	10-0-10
<i>sp.</i> ⁶										
Rainfall in inches										
Normal	18.04	21.42	19.87	15.27	6.91	2.79	0.37	0.21	0.22	0.32
1932-1933	24.24	24.25	11.25	11.92	9.66	0.68	0.39	0.	0.	0.62

on the third of the month in 1931 but not until the seventeenth in 1933. However, in 1924, two specimens were found late in June.

Many species disappeared from strata of earthworm activity before the end of the academic year: In September, *Plutellus pandus* and *Eutyphoeus rarus*; in October, *Pheretima alexandri* and *Eutyphoeus peguanus*; in November, *P. anomala* and *E. foveatus* (only one specimen of each secured in that month); in January, *Drawida abscisa*, *D. rangoonensis*, *D. rara*, *Pheretima campanulata*, *P. houllèti*, *P. planata*; and in February, *P. peguana* (but only 44 specimens obtained in November-February as compared with 220 in October). These same species vanished, almost without exception, in other years. Variant times of disappearance for the academic year 1924-1925, as shown by regular sampling (5600+ specimens identified) from another and much larger portion of the municipal area were as follows: in October, *E. foveatus*; in November, *P. peguana*, *P. alexandri* and *E. peguanus* (only 4 specimens of the last two species found); in December, *P. anomala* (but only 13 specimens found in November-December); and in January, *D. papillifer*. Of that last species an occasional individual still could be found at Kokine in March, 1933, but through all the months after September only 13 individuals were found. Similarly, nine specimens of *P. houllèti* were obtained during February-March, 1924. After September, in each year, much more soil had to be dug over to secure fewer specimens of those species than in previous months. Activity clearly ends for most of these worms before November and nearly always, even for exceptional individuals, before the end of March. Not until late in May, at the earliest, were any of those species ever found again. By early June, earthworms were to be found almost everywhere although *P. anomala* appeared only in July.

¹ The year is divided in Burma into two major seasons: the rainy, May-October and the dry, November-March. The dry period is popularly subdivided into a cool (plains) or cold (hills) season, November-February and the hot season, March-May

² The number of individuals collected in each of three recognized age classes: 7-, juveniles, without sex markings; -0-, acitellates, with external sex markings but lacking a clitellum; -2-, clitellates, clitellar development obviously under way or completed. Zeros are omitted whenever feasible.

³ Includes some postsexual individuals in which the clitellum has undergone more or less regression. Porophores and genital markings may also undergo some regression.

⁴ Clitellate specimens of *D. gracilis* never were found in Rangoon. One anterior portion of a clitellate individual was obtained from an unknown site elsewhere by a local collector.

⁵ *P. elongata* is very rare in Rangoon where soil conditions may be unsuitable. This exotic species flourishes, in India as well as Burma, in black earths and good cotton soils.

⁶ Identifications of species of *Glyphidrilus* (at least two) and of dwarf forms, those with a maximum thickness of 1-2 mm (of which 14 already are known to be present in Rangoon) had not been completed when war ended the investigation of Burmese earthworms locally.

Eight species were procurable through October-March, 1932-1933 and in other years during April-May. For each of those forms, as a species, there obviously need be no seasonally determined period of inactivity. Three species are restricted as to habitat, the glyphi-driles to ooze and mud throughout the year, *Perionyx excavatus* to organic matter and to sites rich in manure, garbage, compost or other plant debris which must be moist. Four species are confined, from January to middle of May or later, to ghats where dhobies beat the laundry of the city against their rock slabs, small areas around wells and hydrants where people bathe, drainage ditches, margins of ponds, tanks, lakes, sites receiving waste effluents from bathrooms and cookhouses. The eighth species was found in the same period only in sand or sandy soil that remained moist. Water obviously is a major factor in controlling horizontal distribution during a considerable portion of the year and in that period continuation of activity for many individuals and several species is allowed only by such moisture as is accidentally provided at the surface of the soil by man. Monsoon moisture equally obviously, as a glance at the rainfall figures in the table will show, must be a major factor in controlling activity throughout most of the area. Considerable rain seems to be necessary, in the clays and iron-rich, laterite-derived soils of Rangoon, to enable return to activity. Not until late in a month with a normal rainfall of 11.98 inches do worms begin to appear. In May 1924, with a 2.44 inch deficit, *E. foveatus* was not found at all and even at end of the month other species were not common. In May 1925, with 5.41 inches more of rain, *E. foveatus* was readily obtainable almost anywhere and greater numbers of other species were active than in the previous year. Near saturation of the air during June-August might be expected to favor considerable activity on the soil surface. Castings, deposited there by species of *Eutyphoeus*, *Lampito* and some of the pheretimas, are obvious nearly everywhere one looks, but subterranean feeding and copulation seem to be the rule. Strayed individuals occasionally were seen wandering on the surface during daylight hours but only after heavy rain. However, *P. excavatus* must take advantage of the atmospheric moisture to explore the megadrile equivalent of outer space as it was found in trees and on roofs of buildings as high as four stories. Several of the small species that are not considered herein, dichogasters especially, also indulge in similar feats.

As the rainfall decreases and number of sunny hours increases in September, but more especially in October-November, soil that is not kept moist artificially dries. As it hardened the worms disappeared. Species of *Eutyphoeus* abandoned even the wet surface strata where *L. mauritii*, *Octochaetoides surensis* and *Drawida longatria* appear to aggregate. The wide-wandering *P. excavatus* often finds refuge during the drouth in submerged vegetation. Least moisture seems to be required by *Pontoscolex corethrurus* but eventually worms of that species empty the gut and, each coiled tightly into a ball

within a closed chamber several inches below the surface, remain for an unknown time in a state sometimes called diapause. That term is used hereinafter for worms in the condition just described but without reference to any other characteristic such as water content.

Reaction to seasonal decrease in precipitation accordingly varies interspecifically as well sometimes as intraspecifically.

All worms secured in June 1932, except a few individuals of four species, were juvenile. Only in July or even later were adults of other species obtained. Records still available for 1933 show that in the same area clitellate specimens were first secured as follows: Early in June, *L. mauritii*. Last week of June, *Plutellus pandus*. In July, *Pheretima peguana* in the first week, *E. foveatus* on the 7th day, *O. surensis* on the 14th, *P. posthuma* on the 16th, *E. rarus* on the 20th, *E. peguanus* on the 23rd, *Drawida longatria* and *P. houlleti* in the last two weeks. In August, *D. rangoonensis*, *rara*, *P. alexandri*, *P. anomala* (on the 17th) and *P. campanulata*. In October, *D. papillifer* and *P. planata*.

Appearance of the first macroscopically recognizable epidermal differentiations that allow a specimen to be listed as clitellate, does not, of course, show that the worm is ready to breed. One to several additional weeks may be required. Maximal tumescence of the clitellum doubtless is correlated with full maturity, but whether the yellow, orange or red coloration that may become visible in the thickened epidermis is associated primarily with function or regression is unknown. Definite dates for beginning of breeding cannot now be stated, but in most individuals of many species sperm were not accumulated on male gonoducal funnels ready for discharge during copulation until late in August or early in September. Breeding of terricolous species must then be limited rather generally to the period from the middle of July to the middle of October, but for many individuals of most of these forms to several weeks in September. Breeding, so far as could be deduced from presence of a seemingly functional clitellum, appeared to be possible at any time for *Perionyx excavatus*, *L. mauritii* and *O. surensis*. Confirmation for *P. excavatus* was provided subsequently by finding individuals with aggregated sperm on male gonoducal funnels in every month of the year. Cocoon deposition in the laboratory during December-January and the finding of cocoons outside from September until the end of March hints that *Pontoscolex corethrurus* may be similarly uninhibited. During nine months of the year at least, *Pheretima posthuma* is able to breed but cocoons were not deposited in the laboratory and there the clitellum soon disappeared. Glyphidile cocoons were found only during March-April. However, uninterrupted breeding of these limicolous species is indicated by size of juveniles that were obtained throughout the year.

Individuals of five species, *D. longatria*, *O. surensis*, *Perionyx excavatus*, *L. mauritii* and *Pheretima posthuma* remained active, in favorable conditions, after the clitellum had regressed. Late in May

or early in June some few specimens of those species usually could be found with the marks of regression still recognizable. Accordingly, a second breeding season for such individuals as survive the drouth seems possible but has not yet been demonstrated in laboratory controls.

Of the early disappearing species, *P. pandus*, *E. foveatus*, *E. peguanus* and *E. rarus* are endemic. Of the species that are active into March, *D. gracilis*, *D. longatria*, *D. papillifer* and the glyphidriles are endemic. The others, *O. surensis*, *Perionyx excavatus*, *L. mauritii*, *Pheretima posthuma*, and *Pontoscolex corethrurus*, like most of the omitted small species, are exotic and were introduced by man. No information is available as to seasonal periodicity in their original homes some of which are unknown.

BURMA

Several hundred thousand Burmese earthworms collected outside of Rangoon in 1922-1940 provided data that enable the following generalizations. From the southernmost tip of the country to the foothills of the Himalayas, the rainy season is the period of activity for terricolous earthworms. On the Shan Plateau, at elevations of 4000 feet and more, casting deposition on the surface, especially by giant species of *Tonoscolex* (Gates, 1927) testified to much ingestion of soil during May. Contrariwise, similar activity in the dry zone of central Burma was recognized later than in Rangoon. However, on the porous soil of that zone less precipitation seems to stimulate the worms sooner. Thus, after the first seven days of rain, characteristic tower-like castings in great abundance dramatically demonstrated almost over night that feeding had begun again by species of *Eutyphoeus*. In the western hills, Dr. G. Heinrich was able to find specimens of the same genus after only two rainy days. Duration of activity accordingly may be shortened or lengthened locally by soil structure, elevation and variation in amount of precipitation. Species of *Eutyphoeus* disappear toward end of the rains just as in Rangoon; in Akyab for instance, the earthworms disappeared even during September and October with 22 and 11 inches of rain, respectively. Occasional individuals of other endemic forms may remain active for several more weeks especially in dense jungle shade, under accumulations of litter and in other sites where for one reason or another soil dries less rapidly. Horizontal distribution during the latter part of the dry season is markedly discontinuous as in Rangoon and activity is restricted to strata that remain wet and restricted in part because of human activity. Worms found at such sites in January-April are apt to be mostly exotic. Endemics usually are referable to species of *Drawida*. Foreign species, in addition to those already listed from similar sites in Rangoon, include Chinese forms and one lumbricid supposedly from northeastern United States.

Breeding, as evidenced by maximal tumescence of the clitellum and by aggregated sperm on male funnels, rather generally through-

out the country and certainly for most individuals of many terricolous species, is restricted to a single period centered in September. At higher elevations, in a northern portion of the Shan Plateau, the reproductive period may be quite definitely later in the calendar year, possibly because of the lower temperatures. Maturity, in most of the medium-sized species, probably is attained during the breeding season of the next year. Giant species of *Tonoscolex* in the lowlands, according to available evidence, cannot be expected to breed even at end of the second year, possibly not until the fourth.

The limicolous glyphidriles are known to be active on the Shan Plateau through the dry season and in the lowlands of the mid-longitudinal third of Burma during the rains. Destruction of records and collections during World War II prohibits any statement as to breeding except that in Victoria Lake cocoons were deposited on or above the surface of the bottom ooze. Some at least of the hatchlings must feed for a time near the banks before moving to sites that were not investigated.

Two sorts of unusual activity also are seasonal. "Mass migrations" were not seen by the author but they often have been observed by government officials and missionaries while traveling along the mule tracks of the western hills. All written and oral reports agree in the following particulars.—At the beginning (October-November) of the cold season, in a region where mountains are covered with a thick undergrowth of mosses and ferns, worms crawl on the surface early in the morning in huge numbers. As they drop down from the upper bank they almost cover the road. Direction of travel, whether on the track or at either side, is always downhill. In the evening not a worm is to be found.—The assumption usually made was that the annelids were in search of more adequate supplies of water. A number of migrating individuals were preserved. All were referable to the genus *Perionyx* but were immature and could not be further identified.

"Mortal wanderings" have been observed, sometimes for several days in succession, only after the rains had ended and, indeed, after activity in the hardening soil rather generally had ceased. Hours of emergence are unknown but the wanderers were found, early in the morning on roads, paths, in almost any open place. Sooner or later locomotion ceased and the worms dried up. Individuals that were preserved proved to be fully mature. All of them belonged to endemic species of *Eutyphoeus*, *Desmogaster* or *Pheretima* some of which have been collected but rarely. One desmogaster, except for several individuals, is known only from wanderers that happened to be above ground when someone in the vicinity was looking for them. Residence of these rather large worms, at greater depths than were dug over or in soil made impervious to cool implements by interlacing roots of the rainforest, may be responsible for failure of various attempts to secure material.

During the rains, almost everywhere, in the hills, the plains, even

in the dry zone with only 20-40 inches of rain, earthworms are present in great profusion. Multitudes, in certain parts of the country, do die on the surface early in the dry season but in the next southwest monsoon worms are just as common as previously. Few resting individuals were found in spite of visits at every opportunity to sites where earth was being moved. However, exposed surfaces never were close to the water table.

Everyone in Burma who has given the matter any thought or who has heard comment on earthworm reappearances is sure that the worms go down deep in the soil at end of the rains. Those who dug wells during the dry weather reported finding aggregated earthworms near the water table. The mass always was characterized as a "ball" and its thickness was variously estimated to be six to twelve inches. Such balls never became available to the author for examination. However, live worms placed individually in the same receptacle always aggregated, regardless of species differences, in a closely intertwined cluster that often required some effort to disentangle. A clump of a dozen or so specimens has been observed on countless occasions, in the laboratory and after appropriate stimulation, to assume a shape comparable to that of a ball. Similar but possibly larger clumps were said by various individuals to have been seen in heavily flooded areas. There are then good reasons, including some not mentioned above, for believing that many Burmese species do pass the drouth in more or less tightly clustered aggregations.

Hibernation and estivation are not strictly applicable in Burma as the period of inactivity comprises both cool or cold (according to elevation) and hot seasons (*cf.* Footnote 1, Table I).

ALLAHABAD AND NORTHERN INDIA

Our knowledge of the earthworm ecology at Allahabad comes from a thirty-month survey that provided some 25,000 specimens and more especially from the 15,000 that were obtained by regular collecting, weekly during July-November 1943 and fortnightly during December-May 1943-1944. Some of the results of that study already have been published (Gates, 1945, 1947).

The earthworm year begins at Allahabad in July, at least one month later than in Rangoon. By the end of September the worm population near the surface already was decreasing. From the first of October more hours increasingly had to be spent in digging to secure fewer specimens than previously and by the end of the month three species had disappeared. Two more vanished in November and only 16 specimens of *Eutyphoeus* (2 species) were obtained in December. Even the exotic *L. mauritii* which flourishes during the hot months in artificially wetted habitats of arid central Burma was not to be found at Allahabad in January-June. For seven endemics including the three species of *Eutyphoeus*, three to four months of activity are followed by eight to nine months of inactivity. As the worms are quiescent during both cold and hot seasons, hibernestiva-

tion, or some other words expressing the same idea, alone is applicable. The only resting individuals secured, juveniles of *Bahlia albida*, were in diapause, each within a small closed chamber in the upper three inches of soil. Major trunks of the vascular system were distended with blood that appeared not to be circulating. Immersion in water (April) straightened the worms almost at once but did not bring them back into activity.

From October through May, earthworms increasingly were restricted to sites by running and standing water or to those that were kept wet by man. In June of 1943 as well as of 1944, a few individuals still could be found but only at one place, between joints of a pipe that was under water in a ditch. Even those species that linger on after December, whether intruders from the adjacent Deccan or introduced by man, must rest, at Allahabad, during some portion of the year.

Endemic species were not mature in July though seven clitellate specimens of *E. incommodus* were obtained in that month. Sexual individuals, clitellate and with sperm aggregated on male funnels, of *E. incommodus* were found in the first week of August, of *E. waltoni* on August 16 and of *E. nicholsoni* on August 26. Copulation continued, for *E. nicholsoni* and *E. waltoni*, into November. Breeding, as at Rangoon, is centered in some part of September. Adults of *E. incommodus* that had been clitellate and presumably had bred in the previous rain season, were recognized early in July. Life ends, however, for many mature individuals of *E. nicholsoni* and *E. waltoni* in October-November when they are dried by the sun as they wander on the surface in the morning. Again, as in case of mortal wanderings in Burma, these worms showed no macroscopically recognizable indications of disease and were not heavily parasitized.

Other species (perhaps with one exception), according to evidence provided by clitellar tumescence, brilliant spermatozoal iridescence on male funnels, laying and/or presence of hatchlings, breed from July well into the next calendar year. Sexual individuals of five taxa were found as late as the first week in May. Clitellate individuals of the exceptional species, *Plutellus exilis* (presently unknown outside of a single Allahabad quarter), were secured only in November-April and at sites too deeply flooded to be investigated during the rains. Breeding then may be possible, in appropriate conditions, for these species throughout the year. Postsexual active adults of the larger species were obtained from August to May. A second period of breeding appears to be possible for most of the kinds that are thicker than two millimeters but whether any particular individual can breed twice within a single year was not learned.

In the Gangetic alluvial soils of Allahabad, with a pH in the vicinity of 7.5, earthworms appear to be common everywhere during the rains. The three species of *Eutyphoeus* advertise their presence throughout nearly all of the area by erection of tower-like castings. Habits of three other geophagous endemics are unknown. Five ex-

otics also are geophagous but only *L. mauritii* testifies to a wide distribution by characteristic non-tower-like castings. Rarity of one exotic may be due to more recent introduction and two others were found only or mostly (*P. houlletii*) in earth around roots of potted plants. The fifth form, *P. posthuma*, confines itself largely to sands of river banks on which characteristic pellet-like castings are deposited.

The remaining species, including *Plutellus exilis*, are entirely or mostly confined to accumulations of organic matter such as manure, dumps, sites receiving kitchen drainage, ditches carrying waste effluent of human habitations, etc. The single lumbricid was found only at such sites and in flower pots. Little is known about this species, *Bimastos parvus*, in its supposed North American home perhaps because it is primarily a litter-feeding species in some forested region of the great portion of the continent where earthworms never have been collected. A few individuals of geophagous species were found in organic sites. Strays of two organic feeders were found in ordinary soil along with geophagous species.

The humid subtropical climate of Allahabad differs notably from the monsoon tropical climate of Rangoon in precipitation (*ca.* 40 versus *ca.* 100 inches) and in temperature (colder in October-March and hotter in April-June). Most of the rain at Allahabad likewise is monsoonal but falls during June-September. The five inches of June rain is insufficient to bring worms back to the surface and re-appearance in July is gradual rather than dramatic. Greatest activity is during the three months with averages of 12, 10 and 6 inches. October has 2 inches but other monthly averages until June are less than an inch and of no significance to earthworms.

Species of *Eutyphoeus* vanish at end of the rains in Rangoon which is near the eastern boundary of the generic range and also at Allahabad which probably is as near the western boundary of a natural generic range that has been extended somewhat because of transportation by man. All available evidence indicates uniformity throughout the genus. These species were much easier to find during October-November at Allahabad with a rainfall of scarcely three inches than at Akyab and Rangoon with precipitations in the same months respectively of 16 and 9 inches.

No glyphidrilids were secured in Allahabad by considerable digging although a very few, all young juveniles, were found in adjacent areas. However, at one site on a river bank in the Himalayan Terai, 135 specimens (110 clitellate) were obtained late in October but only at a depth of 18 inches. Lack of collections from similar depths at appropriate sites presumably was responsible for failure to secure clitellate individuals in the Kokine quarter of Rangoon. *D. gracilis*, in the adult stage, now also seems likely to have been restricted to strata not usually investigated in Burma.

The earthworm year, in the Allahabad sector of the Gange-tic Valley, in the Terai and the Dun as well as the Himalayas, so

far as could be learned from wartime observations and collections, also comprises a single period of activity followed by one of quiescence. Duration of each presumably is determined primarily by the climate though postponement of quiescence may be permitted at various sorts of sites and especially at those kept moist by man. To the west, in the plains of the Indus Valley, indigenous species are unknown. The pauper fauna comprises exotics introduced from other parts of Asia (including peninsular India), Malaysia, Europe and America. Further observations and comments on the earthworms of west Pakistan and adjacent portions of Hindustan are omitted as a survey now under way in Lahore is expected to provide more substantial support for interesting conclusions.

THE MALAY PENINSULA

This area has a humid, equatorial climate commonly said to be characterized by a constantly high temperature and heavy rainfall throughout the year. The range of annual temperatures at Singapore is only 3-4° F. and monthly rainfall is 6-10 inches. In such circumstances one might expect earthworms to be as common all the time as in Burma during the rains and activity to be possible for terrestrial as well as limicolous species throughout the calendar year. Nevertheless, earthworms were hard to find at Singapore and vicinity on several occasions and no evidence of widespread casting deposition was recognized.

Although annual temperature ranges are slight, the diurnal may be as much as 15-20° and at Singapore the recorded maximum and minimum temperatures, 97° and 66°, are not far from those of Rangoon. Alternating periods of activity and quiescence, though possibly with less regularity than in monsoon climates, now are anticipated but destruction of records during World War II obviates presentation of supporting data.

MAINE, UNITED STATES

A few scattered records of several species, some without locality or other data, constituted hitherto our knowledge of the earthworm fauna of this state. As a result of a study that is still under way, 22 species can be listed from Maine. All are present in the central portion of the state that is now under consideration. Eight, found during twelve years search only in greenhouses and conservatories, need little further mention in a contribution primarily concerned with natural climates. Frequent, regular sampling of various sorts of habitats, as at Rangoon and Allahabad, was impossible throughout any single year but the same or adjacent sites have been examined, as often as circumstances permitted, over a period of six or more years. Except as otherwise noted, worms were obtained by digging. Such disturbance of the habitat may have exterminated isolated colonies of rarer species. Chemicals, including potassium permanganate, were used on several occasions. Where needed, data from

collections made by or for the author in other states are cited from unpublished records.

Allolobophora chlorotica, except for two juveniles, was found only in and around gardens, in a dump where garden refuse obviously had been deposited, in outside beds of greenhouses, in five sets of greenhouses at Bangor and Ellsworth. All worms were of the green variety. Nearly as many specimens were obtained from the greenhouses as from all outside sites. Active individuals were obtained outdoors in April-May, October-November (June-July, Massachusetts and Vermont), in greenhouses November-March (August, New York State). Year round activity obviously is possible for the species.

Clitellate individuals were secured outdoors in April-May, October-November (June-July, Massachusetts and Vermont), in greenhouses November, February, March (August, New York State). In each of those months some of the worms were fully clitellate and, as proved by presence of sperm on male funnels and in spermathecae, able to breed, *i.e.*, lay or deposit cocoons (sometimes called capsules by laymen and oothecae by zoologists). Spermatophores, 1-6 per worm, were noticed only in April. These bodies, adhering to the cuticle, seem to be characteristic in the family (Lumbricidae) to which all our outdoor species belong. Lumbricid spermatophores have no function. They were found frequently in the killing fluid and are rubbed off soon after copulation. Their presence on a worm then is proof of recent mating. For this species, year round breeding seems to be possible in appropriate conditions.

Resting individuals were not found, but estivation and hibernation must be necessary in Maine at outdoor sites.

Allolobophora longa has been found more often than *A. chlorotica*, not only in turf, lawns, gardens and flower beds but also in some fields and pastures further from habitations, in soil of flower pots from private residences as well as in four sets of Bangor greenhouses from one of which it was secured several years in succession. Active individuals were found outdoors in each month of March-December; postsexual a clitellate adults in March, April, June, August, October and November; clitellate adults in April-May as well as the first few days in June, October-December; a clitellate adults in April-July and September-October; juveniles in April-December and in greenhouses November-February. Year-round activity obviously is possible for the species. Active worms collected between the middle of June and the end of September were from the following sites; under turf of a copiously watered lawn (September), densely shaded and wet litter (August), a gulley with water (July), swampy river banks. In open areas not artificially supplied with water no worms were found during the summer.

Spermatophores were seen in October-December and in April, in the latter month on one worm from a site where the ground still was frozen at a depth of an inch. Six of seven clitellate speci-

mens secured October 13 had no spermatophores. Five of the worms, of course including the one with spermatophores, had copulated and presumably were ready to lay. The other two, as indicated by the massed sperm on male funnels, were ready to copulate but had not yet done so. Each of 22 clitellate specimens secured November 19 from the same site had copulated. Sperm not extruded during breeding presumably are lysed as none has been found in postsexual acitellates at end of hibernation or estivation. The single active clitellate worm secured in September (from watered turf) was not in condition to copulate or reproduce.

Although year-round activity seems possible, in appropriate conditions, breeding cannot yet be so characterized. As postsexual worms can be arranged in series, decreasingly showing evidence of previous functioning to early stages of spermatogenesis, individuals that presumably had layed in the previous season should again be able to reproduce.

Juvenile and postsexual worms in diapause were found during September 2-3 inches below the soil surface of open areas. Hibernating individuals have not yet been found at any level.

Allolobophora tuberculata probably is the most common species in Maine where it has been found in peat (the only species), manure (once), under cowpats in pastures, in hen and cowyards, matted leaves, compost, city dump, on city roads and sidewalks in spring after heavy rain, in swampy brook and stream banks, river banks, leaves and mud under two feet of water, under logs in stream beds, in turf, lawns, gardens, pastures, fields, forests, 11 sets of greenhouses at Orono, Bangor and Bar Harbor. Active individuals were found outdoors April-December and in greenhouses October-March. Year-round activity obviously is possible for the species. Most of the active worms secured June-September were from damp or wet sites. Gardens provided a very few specimens in July and September but searching in other open areas was fruitless.

Juvenile and clitellate worms were obtained in every month of the year, postsexual acitellates in each month except February. Spermatophores were noted April-May and October-December. Copulation was seen only in the spring. In one clitellate sample of an October 13 collection, 25 worms (9 with spermatophores) were able to breed and the remaining 9 were ready to copulate. In a similar sample from an October 20 collection at the same site 26 worms (11 with spermatophores) were able to breed and the other four were ready to copulate. All dissected specimens from a November 19 collection at the same site were in a condition to lay. Certainly, most of the breeding of this species in Maine, because of more limited activity in other seasons, is during April-May and October-December. In the forests of Piscataquis County where the season on June 27 was at least a month later than in Bangor, worms were not yet mature enough to copulate.

Estivating worms found several inches below soil surface of open

fields in September were in a state of diapause. Resting worms at other sites, in the upper four inches of soil in summer but much deeper down in winter, were damaged by the machinery that exposed them. Movements of estivating worms (perhaps not in diapause) hinted that those animals, if not mutilated, could have crawled away immediately on exposure. A second breeding season for particular individuals was indicated by the same evidence as for *longa*.

Allolobophora turgida is not common but has been found more often than *A. chlorotica* and in compost, leaf litter, waste land, at the city dump, a stream bank, a river bank, a pasture spring near a farmhouse, turf from a lawn (1 specimen), sidewalk after rain (1 specimen), abandoned grape arbor (1 specimen), flower beds, gardens, outside greenhouse beds and in four sets of greenhouses at Bangor, Ellsworth and Bar Harbor. Samples of more than 20 specimens were obtained only from two flower beds, a long abandoned garden site, one compost heap, the city dump and moist humus in the University of Maine forest at Orono. Except at that last site, the stream bank and the pasture spring, each colonization obviously can be attributable to transportation by man. Active individuals were found outdoors April-June and August-December and at greenhouses in January. Nearly all of the June-September specimens were from sites that were moist or wet. Year round activity is possible, in appropriate conditions, for the species.

Clitellate individuals were found April-June, August, October-December and in January at a greenhouse, June and August specimens in brook and river banks. Spermatophores were noted April-May, August and October. Copulation was seen only in the spring. Dissections of clitellate samples show that some worms were ready to breed in each of the months during which the species was found.

The only estivating specimen secured (September) was in a state of diapause. Hibernating specimens, from the site of a former garden, were obtained at greater depths but were considerably mutilated by the machinery that exposed them.

Dendrobaena octaedra is rare in central Maine where it was found only at twelve places, three in Bangor, two in Dedham and one each in seven other townships. Sites were swampy stream and brook banks, under elm logs, in leaves of roadside gulleys and ditches with water, compost (1 specimen), in and under leaf litter in woods. Prior to the present study this species had been found by the author in manure piles of several counties. Although two samples were from forests in unsettled sections of Piscataquis County, both were from vicinity of former habitations to one of which exotic plants are known to have been introduced by a well-to-do man locally reputed to have been a smuggler. Presence at some of the other sites obviously is attributable to transport by man. Active individuals were found, in April-October, at a site that has been under observation for eight years and were secured from localities outside

Maine in November-December. Year round activity presumably is possible for the species where conditions permit.

Clitellate specimens were obtained in April-August and October. Cocoons were deposited in damp leaf litter during July-August. Reproduction is parthenogenetic.

Quiescence during the winter in Maine obviously is necessary and a juvenile found in aggregated silty clay dug up from unknown depths after the ground had frozen in November probably was hibernating.

Dendrobaena rubida was found more commonly and in larger numbers than *D. octaedra*, in sandy loam four and one-half feet below ground level in unfloored cellar of a dwelling house, in toilet bowl of another residence, black earth of brook and stream banks, saturated soil around a pasture spring, under logs in a pasture, under elm logs, under stones in woods, in cowyards, manure piles, powdery black soil where manure formerly had been piled, compost, matted leaves at a dump, leaf litter and humus in forests, culture beds of an earthworm farm and six sets of greenhouses in Orono, Bangor and Ellsworth. Active individuals were found outdoors April-December and in greenhouses October-March. For this species year round activity, in appropriate conditions, obviously is possible.

Clitellate individuals were found outdoors April-December and in greenhouses October-February. Spermatophores (containing sperm) were found on outdoor worms April-May and October-December, on greenhouse worms October-March. In each of the months in which clitellate worms were obtained, presence of sperm on male funnels, and in seminal receptacles as well as the clitellar tumescence, indicated readiness to lay. Breeding certainly appears to be possible through so much of the year as temperature permits.

Quiescent individuals were not found, but at some of the sites hibernation within the soil is probable. The owner of the cellar mentioned above insisted that entrance could have been gained only by burrowing down from the outside and then under the foundations of the house.

Parthenogenetic morphs of the species are present in central Maine but more rarely and in fewer numbers.

Eisenia foetida, the brandling, was secured from manure, compost and matted leaves at 12, 3 and 4 sites respectively and in 6 sets of greenhouses at Bangor, Ellsworth and Bar Harbor. Active individuals were found outdoors March-July and September-November. Some were clitellate in March, May, July, October-November. This species is raised for sale at three "earthworm farms" in central Maine. Breeding, as indicated by maximal clitellar tumescence, presence of sperm in seminal receptacles as well as on male funnels and by cocoon deposition, is year round for the species in habitats providing appropriate temperature, moisture and food.

The local distribution obviously is in part due to human activity but some of the finds seem to indicate a propensity for wander-

ing. Several months after departure of a circus the species was found in a pile of elephant droppings. The nearest site at which other specimens could be found was a greenhouse manure pile more than a quarter of a mile away. One individual entered a leaf-filled open wood box held six inches above the ground by stones. Artificial fertilizers had been used in nearby gardens and flower beds where *E. foetida* was not found. Again the nearest known site was a greenhouse but this time a mile away. However, some of the gardens in the intervening area could have been manured.

Eisenia rosea seems to be nearly as common as *A. tuberculata* and was found in forests, fields, pastures, cowyards, gardens, lawns, on roads and sidewalks after heavy spring rain, in a city dump, waste land, under rocks and logs in open areas, in compost, in and under matted leaves and at 8 sets of greenhouses in Orono, Bangor, Ellsworth and Bar Harbor. Many of the sites were unusually damp for the season or even saturated but others appeared to be rather dry. Active individuals were found outside during April-December and in greenhouses October-March. Year-round activity again seems possible for the species where external conditions permit it.

Clitellate adults were secured outside, April-July, September-November and in greenhouses October-March. Cocoons were not found. A yellow coloration of the clitellum that persists as tumescence disappears may prove to be associated only with regression after breeding has ceased. The species is represented in central Maine, so far as could be discovered, only by male sterile morphs. As reproduction must be parthenogenetic the only available evidence of readiness to lay, until the ovaries can be studied, is that provided by the thickness of the clitellar epidermis. Assuming then that near maximal or maximal tumescence of the clitellum does indicate ability to lay, breeding appears to be possible, for the species, throughout the year.

Resting individuals were not found though hibernation and estivation must be necessary for much of the population.

Eiseniella tetraedra is uncommon in central Maine where it usually was found in mud under water or in saturated soil (black) of stream, brook and lake banks. One colony is present in the mud around a pasture spring far from any brook or pond but fairly near a farmhouse. A few individuals, one in a flower bed outside a Bangor greenhouse and three under elm logs in a well drained pasture, appear to have strayed from their usual habitat. Four specimens were found in an Ellsworth greenhouse.

Active individuals were obtained in April-July and October. Clitellate adults were secured in May-July. Spermatophores, all without sperm, were found on four worms in March and one in June. Scattered specks of iridescence on male funnels showed that few sperm had been matured. The species is represented in Maine only by an athecal morph. Parthenogenetic reproduction is probable.

Resting individuals were not found but subsequent reappearances

at a site from which all active worms had been removed may be indicative of existence of a quiescent stage.

Lumbricus castaneus is fairly common in central Maine where it was found in and under matted leaves at a city dump, leaf litter and humus in woods, leaf piles, in leaves of roadside gulleys and ditches with water, in compost, manure (once), finely powdery black soil near a manure pile, cowyards, under timber and cowpats in pastures, stones, logs, in saturated soil by pasture spring, in saturated black soil of stream and brook banks, in turf of lawn (2 specimens), in cellophane-wrapped lettuce purchased at a supermarket December 23, in a flower pot at a residence, in outside beds of greenhouses and in four sets of greenhouses at Orono, Bangor and Ellsworth. Active individuals were found outside, March-December and in greenhouses October-March. Year round activity, in appropriate conditions, obviously is possible for the species.

Clitellate individuals in a breeding state were secured outside, March-December and in greenhouses during March. Year round breeding, in appropriate conditions, seems possible for the species.

Hibernation must be necessary at many of the sites. Active clitellate specimens from aggregated silty clay recently dug up from unknown depths after the ground had frozen probably had been quiescent. These worms and a juvenile of *Dendrobaena octaedra* or their ancestors may have been taken to the cemetery along with some of the numerous potted plants.

Lumbricus rubellus is rare in central Maine where but 36 specimens were found at seven places during the last twelve years. Sites were swampy stream bank, under cowpats in pasture some distance from farmhouse, under stones and boards in cowyard near another farmhouse, in moist humus and litter of the University of Maine forest, a garden and one city street after a heavy rain in October (2 specimens). Active individuals were found in June-July and October-November. The July worms were from damp soil in Piscataquis County forests but near sites of former habitations.

Clitellate individuals, in a condition to lay, were found in June-July, October-November and in other states (Gates, MS) during March-May, September and December. For this species breeding appears to be possible, in appropriate conditions, throughout the year.

Resting individuals were not secured but hibernation must be necessary at each of the Maine sites.

Lumbricus terrestris, the dew worm, night-walker or night-crawler, probably is about as common as *A. tuberculata*. It has been found in aggregated silty clay, fine powdery black soil, sandy loam, sand mixed with organic matter and in weathered glacial debris primarily from shales and granitic materials. Sites include almost every open area such as lawns, gardens, fields, pastures, bare ground, waste land by river, golf greens and golf courses, also on city streets and sidewalks in April, May and November after heavy rain, in saturated

soil by brook and stream banks as well as by a pasture spring, in a cellar (cf. *D. rubida* above), under stones and elm logs, in cow-yards, leaf piles, matted leaves at city dump, compost, under cow-pats in pastures, in culture beds of an earthworm farm and in five sets of greenhouses (juveniles only) in Bangor and Bar Harbor. Of 317 specimens secured from under cow pats and in other organic matter, 20 were adult and 297 were juvenile. Thirteen of the adults were in a breeding stage and only one of them was found in each of the sites. Cocoons were not found in the organic materials in which juveniles now appear to aggregate after hatching.

Clitellate individuals in a condition to breed were found outdoors in March-December. Copulation was noted every time worms were seen in activity at the surface during the night. Active juveniles were found in greenhouses during November-March. Breeding presumably could be, in appropriate conditions, year round for the species.

On hot and dry summer nights these worms do not come to the surface unless the turf is watered but they do emerge as soon as dew or fog provides the required moisture. Presumably then, estivation is inapplicable to the state of worms that have only temporarily withdrawn to unknown depths. Enforced cessation of activity at the surface in the winter perhaps can be called hibernation until it has been possible to learn just what happens at that time. Activity at the surface is resumed, as noted below, while the soil is still frozen.

Octolasion cyaneum, previously known in North America only from a Boston garden and arboretum, is very rare in central Maine where 37 specimens were obtained at six sites, five of which are in Bangor. Habitats include grape arbor of an abandoned estate, flower bed, in or adjacent to a long abandoned garden and two sets of greenhouses (13 specimens). The sixth site, in Dedham, is a leaf pile beside the camp of owner of the Bangor garden. Active individuals were found outside, April-May, August (ground damp, bare and completely shaded from direct sunlight), October-November, in greenhouses October and January. Clitellate individuals were found in May, August, October-November. Reproduction is parthenogenetic.

Hibernation is necessary at each of the sites and estivation at some of them.

Octolasion lacteum is not as rare as *O. cyaneum*, having been found at one place in each of nine townships. Sites include a garden (once), humus in University of Maine forest, clayey soil in forest cutting, in mud near cat tails by lake, in brook and stream banks. Except at two places, one of which is a garden, the sites were damp to saturated. However, a second Orrington site was in a very dry, alder overgrown pasture where two specimens were obtained in October.

Active clitellate individuals were secured in May-July, September-

October and outside Maine in August and November. Reproduction is parthenogenetic, at least in Maine, because of male sterility.

Hibernation is necessary at each of the Maine sites. Sampling may have exterminated certain colonies but estivation is anticipated for worms in such places as do not remain wet during the summer.

DISCUSSION

Any earthworm fauna native to Maine was exterminated during the ice ages. All outdoor species are exotic, of north European origin and doubtless were introduced since 1492. Indeed, persons now living remember when earthworms were unknown in their Aroostook County townships from which the glaciers are said to have disappeared 10-11,000 years ago. Some of those men recall deliberate introductions primarily to provide a supply of bait. Records also have been found of earthworms being introduced into southwestern and western Maine by anglers. For every such instance that can now be cited there must have been very many others that never will be known. Of greater importance even than anglers have been horticulturists and floriculturists. Fruit trees early were imported to Massachusetts by Governor Endicott and to New York by Peter Stuyvesant. Apple trees and lilacs near cellar holes of so many abandoned Maine farms testify at least to a possibility of numerous introductions. When economic circumstances enabled support of floriculture locally, more or less permanent sources of earthworm dissemination were established. Worms brought from many parts of the world in soil with potted plants were protected from inclement weather in greenhouses and conservatories, permitted to multiply for several years and then were taken outside in the discarded soil. Some, however, remained in out of the way corners and under plant benches to infect the new soil that was brought in. Even today, in spite of steam sterilization, insecticides, chemical fertilizers and modern techniques, eight exotic species that have been unable to colonize outdoors linger on in the artificial habitats to which they were brought some time back, certainly in some cases more than twenty years ago. Exotics, in one greenhouse, even survived a fire that destroyed the superstructure.

Since 1935 earthworm farms may have become a much more important source of dissemination than the greenhouse industry though for fewer species. Three of the commonly cultured forms are lumbricid and can establish themselves throughout much of the United States and Canada. The fourth, which was raised for a time by a Maine dealer, is a tropical species of the African family Eudrilidae! Although purchased primarily by anglers who are likely to scatter them in all sorts of out of the way places, the earthworms are also sold to organic gardeners and farmers to improve soil fertility. The culch that is discarded from breeding beds and sold for fertilizer often contains many cocoons.

All of the forms, after expulsion from the ivied aisles of a hot-

house environment, are not able to spread uniformly in every direction. Dietary preferences now appear to be an important factor in determining horizontal distribution and they allow the fourteen Maine species to be catalogued in three groups.

1) Geophagous, including *A. chlorotica*, *A. longa*, *A. tuberculata*, *A. turgida*, *E. rosea*, *L. terrestris*, *O. cyaneum* and *O. lacteum*. Of these, only *L. terrestris* copulates at the surface and though adults do seem to feed there the gut always is partly and often largely filled with earth. Kinds of soil and their pH appear to be of little significance. Each species has been found by the author in habitats with a low pH of 4.5-5.5. These worms, after omission of the little *E. rosea* and *A. chlorotica*, are just those forms used, in days before bait dealers were omnipresent, by the angler who did not have access to a manure pile and so had to get his bait in a garden. Turf, found to contain the night crawler and three species of *Allolobophora*, long has been moved about locally by man. More recently, as golf became popular and trucks common, sod has been transported to greater distances. Cocoons have been found in earth on machines that are carried about for making or modifying golf courses. Group 1 contains the species that are most widely distributed and most common in central Maine. Similar distributions are likely to have been obtained by these forms in other glaciated areas of North America.

2) Limiphagous or limicolous (mud eating or mud inhabiting), in Maine including only *E. tetraedra*, though occasional individuals of some Group 1 species appear to be at home in mud well under water or in saturated soils. In other places, e.g., New York State and England, *A. chlorotica* may be limicolous at some sites. Occasional strays of *E. tetraedra* were found feeding on drier earth instead of mud. Such adaptability presumably is advantageous after introduction to a new area.

3) Litter feeding, including *E. foetida*, *D. octaedra*, *D. rubida*, *L. castaneus* and *L. rubellus*. Litter here is understood to include accumulations of any kind of organic matter. One of these species, *E. foetida*, doubtless originally a feeder on leaf litter was so successful in colonizing manure heaps as to be commonly known as "the" manure worm. Preference for manure has seemed so strong that in Sweden (Julin, 1949) the species is called haemerobiontic, i.e., entirely dependent on culture. However, some earthworm farmers have found that *E. foetida* does quite well in culture beds with little or no animal matter. In Himalayan hill stations to which it was introduced the species thrives wonderfully well with little if any animal food. From the manure heaps of Maine the worms and their cocoons are, of course, distributed by the farmer onto his fields and pastures at more or less regular intervals. The farmer sells other worms and cocoons to florists who put them into pots that go to many diverse

places including cemeteries on Memorial Day. The farmer also provides worms and cocoons, again of course in the manure, to town and city dwellers for indoor pots as well as outdoor flower beds and gardens. The transportation thus provided during centuries may have been of as much if not greater significance for the species than its own wandering propensity. *D. rubida* often and *D. octaedra* perhaps less frequently must have been similarly disseminated by the farmer before hay and straw as bedding were replaced by sawdust, chips, etc. A species that climbs trees (*D. rubida*) must wander and litter feeding species probably do — several specimens of *L. castaneus* and *rubellus* were seen at night away from any litter. Compost probably has been of less significance for those two species of *Lumbricus* than manure for *E. foetida* and the dendrobaenas, as in Maine people have made it for their own use. However, *L. castaneus* still was present in flower beds for a period after the compost had been applied. Individuals of geophagous species often get into organic matter and so would also be disseminated as it is used for fertilizer. This may be of more significance to *L. terrestris* as juveniles seem to aggregate in such materials. Contrariwise, litter feeders (cf. *D. rubida* above) may have to ingest considerable soil while burrowing down to unknown levels where they hibernate.

Obviously, any attempt to explain local distributions of earthworms in a glaciated area must give due consideration to the role of the only agent known to be of importance in transporting these animals.

Maine lumbricids originated somewhere in Eurasia and from a northwestern portion of that land mass and adjacent islands have been taken to every part of the world where Europeans have settled, lived or even visited. Although now common in Iceland (and also to some extent even in Greenland and Nova Zemlya), South Africa, southern South America, New Zealand and parts of Australia, permanent domicile has been acquired in the tropics (Gates, 1958) only at elevations above four or five thousand feet. One lumbricid, *Allolobophora trapezoides*, from southern Europe and supposedly common in America was not found in Maine nor is there any valid record of its presence elsewhere in New England. Some of the Maine greenhouse exotics have thriven in English artificial environments for more than a century. During that time many opportunities for outside colonization must have been provided. Yet, those same species have established themselves in southern Europe, states from Virginia south and westward, in tropical Burma, India and Malaya at elevations above 4000 feet. *P. corethrurus* originally from some equatorial portion of America is now widespread throughout the tropics but only in the lowlands. Dietary, soil and moisture preferences cannot be invoked to explain these geographical distributions. More intangible factors of the earthworm environment must be involved.

E. rosea in a breeding stage was found April 9, 1956, under a thin

layer of leaves in an exposed patch surrounded by snow and with frost still in the ground. In a little exposed ridge within a roadside ditch, thirteen active specimens of *A. tuberculata*, *L. castaneus*, *D. octaedra*, *D. rubida* and *L. terrestris* were taken April 7, 1956, four (of *L. castaneus*, *D. octaedra* and *D. rubida*) in a breeding stage. Frost still was present 2-7 inches below the surface of the ridge and snow was 2½ feet deep on either side of it. A specimen of *A. longa* with spermatophores was found on April 20, 1956, at a site where the ground was frozen half an inch below the surface. From nearby litter, with many frost crystals between the leaves, eight individuals (four with spermatophores) of the thecal morph of *D. rubida* were found. Night crawlers were seen after dark March 9, 1957, although the ground was still frozen a little below the surface. A leaf pile with considerable ice, in a lakeside woods on April 19, 1959, had many specimens of *L. terrestris* (juvenile), *E. rosea* and *A. tuberculata* (1 with spermatophores). On a little bare strip, the night of March 18, 1960, several dew-worms and a sexual adult of *L. castaneus* were moving about. Copulating pairs were seen. Snow was 16 inches deep elsewhere. Some of the crawlers were seen to emerge from beneath a thick layer of ice at bottom of an adjacent bank. Melt water from snow and ice is not too cold for many of the Maine lumbricids. Individuals secured at those early dates seemed more responsive to stimuli and to have brighter pigmentation. The brandling, usually thought to be more at home in a warm environment, not only remained vigorous while fasted for three weeks at temperatures below 5° C (Gates, MS) but also in that time regenerated normally and rapidly. In the fall, but late and after trees are bare, worms again are active. Failure of the lumbricids to colonize cultivated areas in tropical lowlands to which they were often introduced is not attributable to the vigor of any competition provided by endemics for in those same areas the equally exotic *P. corethrurus* often has become dominant.

All of which suggests that one important environmental intangible is temperature. Maine lumbricids may have become so habituated to rather low temperatures by millenia of existence just south of European ice sheets as to be unable to perpetuate the species in more equable climates. Certainly in Maine, even for part of the *E. foetida* population, hibernation is required by the climate. Nothing is known about the state in which the winter is spent. Aggregation in balls of dozens to hundreds of individuals has been maintained by laymen, but the author has yet to find some one who had seen such clusters or who had witnessed their exhumation. Duration of winter rest of course varies from one year to another as the ground may freeze early in November or not until late in December. Furthermore, emergence to the surface or return to an active stage may become possible early in March or not until late in April.

Estivation also seems to be imposed, for most individuals of geophagous species, by the Maine climate. This time of rest also is

of variable onset and duration. In a dry spring, worms become hard to find in open areas even in May. Usually summer quiescence is continued through September well into October. Thus, for several species there usually are two periods of activity as well as of breeding in a calendar year. There is, however, a possibility that an unusually cool and wet summer can obviate quiescence or that a dry fall and early freezing can prevent autumnal activity and breeding.

The Maine climate is of the humid continental sort and in the most thoroughly studied section the average annual rainfall is about 40 inches with monthly averages of 3-4 inches. Four inches, in spring and fall, then provides sufficient moisture to enable activity but not in summer months. Only 2.65 inches during October-November is sufficient to permit considerable activity in Allahabad but in Rangoon and Akyab 9 and 16 inches respectively, during those same months, is not enough. In Burma, increasing hours of bright sunshine and hardening of the top soil is associated with decreased activity. In Maine summers the top soil of open areas also hardens.

Reproduction in each species of *Lumbricus* and *Allolobophora* as well as for *Eisenia foetida* is biparental. Parthenogenesis is obligatory, in Maine, for *D. octaedra*, *E. rosea*, *O. cyaneum*, *O. lacteum* and probably also for *E. tetraedra*. In *D. rubida*, uniparental reproduction is of course obligatory for male sterile morphs that are rare and obtainable in but small samples. The thecal morph which was found more often and in larger numbers appears to reproduce sexually. As *E. rosea* is the only really common uniparental form, parthenogenesis and any associated polyploidy has not usually proved to be of such great advantage after introduction, at least in Maine, as has sometimes been thought. Similar findings now are anticipated in other glaciated areas of North America. Not always appreciated in this connection is the fact that a single *ex copula* individual can lay for several weeks and that in some species two or more young may emerge from each cocoon.

Most earthworms, from the dwarf species that are about one millimeter thick to the giants that may be 25 mm thick and six or more feet long, have no special respiratory organs. The skin, accordingly, must always be moist enough to permit respiration. But drouth comes sooner or later in the life history, and perhaps even in the humid tropics, to all earthworms except those living in or able to take refuge in permanently wet sites. Some evidence already is available to show that embryonic development of several species (cf. for instance, Murchie, 1960, p. 205) can be interrupted because of insufficient moisture without detrimental results. A similar capacity seems to be necessary in the monsoon tropics and may well prove to be common in megadrilous oligochaetes when this matter is studied. After hatching, lethal effects of drouth are avoided only by cessation of normal activities. This period of inactivity is passed in a state herein called diapause about which a little information has been recorded or in other states about which nothing is known.

Inactivity also is imposed in northerly portions of the temperate zone during some portion of the winter, but nothing is known about the state in which this period is passed although the literature provides some evidence that several lumbricids are able to survive freezing. These alternations of reduced metabolism and gross or macroscopically recognizable activity occur once a year in monsoon lands and twice a year in Maine. Such recurrences constitute a kind of periodicity but without the calendar precision that dictionary definitions seem to require. In earthworms, the phenomenon because of its association with climatic conditions can have no more regularity than does the weather.

Although such periodicity has for many millenia been forced upon the lumbricids now domiciled in Maine, ten of them (in appropriate conditions) still can remain active throughout the year. Three other species, with data lacking only for several months, probably have retained a similar capacity. The fourteenth lumbricid, *E. tetraedra* (as well as three other Maine species, *E. foetida*, *E. rosea*, *D. rubida*), was found (Omodeo, 1948) in an unspecified section of Italy to be breeding throughout the year. *A. trapezoides*, probably widely distributed in warmer portions of the United States, according to the same author also breeds the year round. *B. parvus*, as indicated by data secured in the Orient, probably also is similarly characterized. Those sixteen lumbricids are the species that have colonized most widely in overseas areas to which European earthworms were transported by man.

Most of the geophagous species that remain active throughout much or all of the year in northern India and in Burma are of foreign origin. Geophagous endemics, in the same areas and with few exceptions, seem to be unable to take advantage of artificially supplied moisture during climatically dry periods.

The basic facts of earthworm periodicity long have been known to jungle dwellers in the orient and to laymen in the occident but more especially perhaps to anglers. However, authors of angling classics, from the anonymous predecessor of the prioress Juliana de Berners to Izaak Walton, who long ago probably could have supplied important information, were more interested in writing about fish and fishing than in recording their observations on earthworms. Few biologists have investigated earthworm ecology in the field and from laboratory data, at least in the case of *A. longa*, were derived erroneous conclusions. Paucity of earthworms, present only in two of several hundred soil samples from the Woods Hole portion of Cape Cod, was attributed (Philips, 1923) to low soil pH. Yet, even during the dry summer months when those observations were being made, lay employees of the Marine Biological Laboratory Supply Department were collecting dew worms and were also able to supply live brandlings. The laboratory derived conclusions (Arrhenius, 1921) that Philips cited were also invalid and pH, at least in most soils,

is now known to be of little importance to various geophagous earthworms. Humus and litter also seem to be of little importance to many species. Tropical soils, for instance, are said to be poor in organic matter yet they support large earthworm populations. Furthermore, at depths where even less organic matter is to be expected, giant species are common not only in Burma but also in India and Ceylon.

Many of the Maine lumbricids (all but five) were for a time included in *Helodrilus*. The genus, *sensu stricto*, never has been found outside Europe and the name in its broad and actually supergeneric sense was abandoned more than thirty years ago by taxonomists. Usage of *Helodrilus*, as a habitat designation in American literature, also was incorrect because of intrageneric variation in dietary preference. Intraspecific variation likewise requires caution or qualification in physiological as well as morphological generalization about earthworms. Texts often convey the impression that these animals drag leaves and other materials into burrows or feed and copulate on the surface. In Maine only night crawlers have been found to engage in such activities. Nevertheless, in some northern states occasional individuals (presumably "jacked" at night while feeding on the surface) of another lumbricid were sold by supply houses as *terrestris* (Gates, MS) with the result that impossible anatomical variation has been recorded for the latter species. Copulation, in the literature, always is between clitellate individuals but acitellate specimens with no signs of postsexual regression occasionally were found on dissection to have their spermathecae fully charged with male gametes. Worms taken in copula have proved, again on dissection, to be male sterile and incapable of exchanging sperm. Spermatophores without sperm have been seen on male sterile worms and spermatophores with sperm on individuals of parthenogenetic morphs that had lost all organs for storage of male gametes. Clitellate and seemingly mature specimens of taxa with obligatory biparental reproduction sometimes have empty spermathecae, naked male gonoducal funnels and no eggs in the ovaries. One Maine lumbricid, *E. tetraedra*, that is said to breed year round in Italy, appears to estivate, according to hitherto available data, in Maine even when the site is saturated. The green variety of the geophagous *A. chlorotica* lives under permanent water at several sites and the red variety is known in the States only from manure. As already noted above, the limicolous *E. tetraedra* was found in unsaturated soils and individuals of geophagous species were found in litter and in mud where they did not have to estivate as would have been necessary in their usual habitat. Such instances and others of a similar sort that can be cited suggest a need for caution in accepting generalizations based on a few laboratory experiments or short studies in limited areas.

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A Population Study of the Gray Fox¹

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ABSTRACT: An attempt was made to analyze some of the component forces of some gray fox populations in northern Florida. The size of the populations studied was determined by the use of an age-ratio-reduction method. In this method the size of the population was indirectly derived by determining the magnitude of the effect on the age ratio of sterilizing a known number of females. A knowledge of the degree of reduction of the age ratio caused by sterilizing these females allowed the calculation of the entire female population. Application of the sex ratio permitted an estimation of the size of the entire fox population.

It was possible to estimate the size of these same populations by several variations of the recapture method (Lincoln Index and Schnabel method) and the removal method. The recapture methods usually gave higher estimates than the age-ratio-reduction method. The estimates of the age-ratio-reduction method indicated a density of slightly less than 3 to 4 foxes per square mile.

From recapture distances, a probable approximate diameter of two miles was estimated for the size of the home range of the gray fox in this region. Groups of foxes of family composition were captured in areas isolated from captures of other foxes and were termed family aggregations. Twenty-one family aggregations were found. The diameters of these family aggregations were in close agreement with the recapture data concerning the estimate of the size of the home range.

This study explores the possibility of estimating the size of a gray fox (*Urocyon cinereoargenteus floridanus*) population by altering the breeding capacity of a known number of females and determining the effect on the age ratio of the population. The size of the population is deduced from the magnitude of this effect. The study also includes investigations of reproduction, mortality, and movement.

The census method is similar to the methods used by Allen (1942), Kelker (1940;1945), and Riordan (1948) in estimating the sizes of populations of game animals that were selectively hunted according to sex. Their method was to compare pre- and post- open season sex ratios after which they computed the size of the populations by the use of knowledge of the number of male and/or female animals killed. Kelker's formulae estimated population sizes for each sex and fawns separately. The age ratio was used to determine the number of fawns, but the observed change takes place in the adults rather than in the young as in the method presented here.

The recapture method (Jackson, 1939) derives an estimate from the proportion of marked individuals in the population. In contrast to the recapture method, the age-ratio-reduction method presented here does not require the recapture of a large number of the pre-

¹ A portion of the author's doctoral dissertation presented to the Division of Vertebrate Ecology, Johns Hopkins University. School of Hygiene and Public Health.

viously trapped animals. The capture and sterilization of a single female reduces the number of juveniles in the coming year's population by nearly five, a large change for a small effort. Foxes are difficult animals to trap and possess considerable ability in learning to avoid traps. This makes the age-ratio-reduction method more useful than the recapture method.

Acknowledgments.—This study was executed under the direction of David E. Davis as part of a study of fox populations supported by a grant from the National Institutes of Health. John E. Wood supervised the study in the field. W. G. Cochran developed the formula used in determining the precision of the estimate. The U. S. Fish and Wildlife Service gave permission to use the Panacea Unit of the St. Marks National Wildlife Refuge as one of the study areas.

To Rudolf Osboldt go especial thanks for co-operation and hospitality far beyond ordinary convention. W. C. Teagle permitted use of his Norias Plantation and Marvin Sasser, the plantation manager, and James Lee and Frank Krine, assistants, co-operated. Likewise thanks are due the late Senator W. E. Edge for permission to use his Sunnyhill Plantation and to Kurt Clemmens the plantation manager.

The Oceanographic Institute of the Florida State University provided the facilities of their marine laboratory. The Florida Game Commission gave permission to trap. O. Earl Frye and Ernest S. Tierkel gave assistance, encouragement and aid. And to my wife, Julia, go my deepest thanks for her unceasing efforts and encouragement from the beginning.

PROCEDURE AND METHODS

In brief the procedure was to catch foxes on an area before the breeding season, mark them, and release them. The females were sterilized by surgical hysterectomy. The juvenile-adult ratio was noted. The purpose of marking was to prevent counting an animal twice. A year later a sample was obtained from the population, duplicating as nearly as possible the trapping effort of the first year. The juvenile-adult ratio was again noted. It was assumed that the decline in the ratio of juveniles to adults was related to the number of females sterilized. The total females in the population were estimated by calculating the number of females required to be sterilized to produce a complete decline in the juvenile ratio to zero. By applying the sex ratio the entire population was determined.

Certain assumptions are made in the age-ratio-reduction method used in this study: (1) the sterilization is complete; (2) the sex and age ratios in the sample are representative of the actual sex and age ratios of the population; (3) there is no immigration or emigration of foxes from the area; (4) the reproductive rate and probability of dying remain constant during the study or changes can be determined and adjusted for; (5) there is no loss of marks on the foxes for the first year; (6) the relative trapability of young and adults does not change during the time of the study; (7) there is no marked change in the behavior of the sterilized females; (8) no other factor, such as climate, changes enough during the time of

the study to affect the age ratio; and (9) the observed reduction in the ratio of juveniles to adults from the first year to the second year was due to the sterilization of the female foxes.

The following efforts were made to check the above numbered assumptions: (1) penned females and recaptured females were examined after a lapse of time; (2) the sex and age ratios were compared with each other and with other populations of foxes from this region (Wood, 1959); (3) a mile wide peripheral area was set up around each experimental area to determine the extent of movement of the foxes, also the region for about 15 miles around the plantation areas was trapped and any massive emigration from the study areas would have shown up in the capture of tagged foxes outside of the study areas, existing natural barriers restricted movement on a third study area; (4) an examination of the age classes of the population and the mortality rates for both years indicated the constancy of reproduction and mortality; (5) the use of the ear tattoo ruled out loss of marking of the foxes; (6) the extent of trap avoidance was determined to a degree by comparing recapture rates of different classes of adults; (7) a number of penned, sterilized females were kept under observation to determine if any marked change in behavior occurred; and (8) an examination of the Weather Bureau data gave a check on the stability of the weather during the two years. These checks are not absolute tests of the degree to which any of the assumptions varied from the expected, however, they were sufficient to detect any serious deviation.

A central area, six square miles in size, was set up for the area wherein the female foxes were to be surgically treated. This area coupled with a one mile wide peripheral area, selected on the basis of the size of the home range (Sheldon, 1950;1953), there resulted a total of 20 square miles for each study area. Two experimental and one reference (control) areas were established.

The size and compactness of the areas required, limited the choice to the Norias and Sunnyhill plantations located between Thomasville, Georgia and Tallahassee, Florida. The Panacea unit of the St. Marks National Wildlife Refuge was chosen for the third study area, because of its apparently high fox population. Boundary difficulties restricted the placement of the study areas on the plantations, resulting in the southern quarter of these two areas having a common peripheral area one and a half miles wide. A large wedge of land lay between the northern ends of these areas, which, although outside the agreed peripheral areas, was also trapped because of its location (Fig. 3). Lake Miccosukee was used in locating the central area on the Norias plantation. However, at the beginning of the study the lake went dry. The lake bed was examined on several occasions and the tracks indicated that few foxes ventured far out. Placement of the study area on the Norias plantation resulted in approximately 20 square miles being trapped and 18 square miles being trapped on the Sunnyhill plantation. The natural barriers

around the Panacea area resulted in only 16 square miles being trapped.

Aerial photographs, obtained from the United States Department of Agriculture, were used to prepare maps of all three areas and to locate all the small roads that were to be trapped. A 0.1 mile grid was placed permanently on the map and cross referenced. The location of every animal trapped was obtained by this cross-reference system to the nearest 0.05 miles.

The trap used to catch the foxes was the Victor Number 2, coil spring, square jaw fox trap, manufactured by the Animal Trap Company of America, Lititz, Pennsylvania. Attempts to prevent injury by steel traps were made by wrapping the jaws in various ways; all proved unsatisfactory. Damage to the leg or foot of the animal was found to be due to escape efforts. To prevent this type of injury, all traps were fastened to a light drag, which would allow the animal to leave the point of capture, but seriously impede progress. A dog, a Golden Retriever, was used to track these animals, which he did with great skill after once learning the procedure. The use of this dog increased the efficiency of the trapping by an estimated thirty per cent.

The set used in trapping was described by Wood (1954). Seventy to one hundred and twenty traps was the usual number of traps in operation. The distance between traps varied slightly, but generally was 0.1 miles. When a road was retrapped, the traps were usually placed at different spots. Traps were run every day and usually left in the ground for seven days. During the hottest weather, scent was applied twice during the week after the initial setting because of excessive evaporation. After every rain, traps were both rescented and reset. By alternating the trapping weeks on the three different areas, a relatively equal trapping effort was made on each area. Trapping was stopped on the Sunnyhill plantation on October 18 and on the Norias plantation on November 18, to allow for dog training prior to quail season. On the Panacea area, trapping was continued until December 18 in 1954 and December 24 in 1955. Trapping began June 14 the first year and June 13 the second year.

The method of altering the age ratio of the population was that of surgical sterilization of the female foxes. The surgical technique followed was similar to the veterinary "spaying" of female dogs, except that in this study only a portion of each uterine horn was removed. Thus the ovaries and portions of the uterus were left intact. It was hoped that this procedure would prevent an alteration in behavior and activities due to endocrine changes. The wound was then sprinkled with Terramycin and coated with collodion to keep screw worm fly larvae out of the wound. The nocturnal habits of the fox were probably more effective than anything in avoiding this hazard. Each fox was given 1 cc (300,000 units) of procaine penicillin in sesame oil intramuscularly. A simple laparotomy was per-

formed on the female foxes from the reference area (Sunnyhill plantation).

The operation on the foxes caught on the plantations was performed in a laboratory in Thomasville, Georgia, on the same day that the fox was caught. Foxes were brought into the laboratory in a burlap sack, through which Nembutal was administered intraperitoneally. After the operation the foxes were placed in small cages to recover from the anesthetic and were released early the following day at the point where they had been captured. The operation on the foxes from the Panacea area was performed in the back of a bakery delivery truck converted for use in running the trap lines.

A method for determining the age of wild foxes was developed by Wood (1958). This method used the constant wear on the molars and the fact that foxes are all born within a short period of time in early spring. Thus foxes caught at any time of the year can be aged with a reasonable degree of accuracy to the month, on the assumption that all foxes are born in March.

In addition to the tooth wear method, the weight of a fox from June until the middle of August will clearly separate the adult foxes from the juveniles, but in the middle of August some juveniles begin approaching six pounds, the minimum weight of some adults. Most female foxes with small mammary nipples are juveniles and those with large nipples are undoubtedly adults. Juvenile foxes have characteristically puppy fur up until about the middle of August. In late summer, when juveniles are approaching adult size, young foxes may be distinguished at a distance by their brightly colored bushy tails. The tail of adults at this season is faded and badly worn, showing a shedding of hair prior to the growth of new hair in fall. In addition to all these factors, it is possible for a worker handling many foxes to know by other, particularly facial, characteristics the difference between young and adult foxes (Fig. 1).

The following data were recorded from all trapped foxes: date of capture, location of capture, sex, age, weight, size of mammae, and presence or absence of milk. At the time of hysterectomy, the number of placental scars was recorded. During the first year of the study all animals were marked with small aluminum ear tags possessing a number and a return address. About half way through the first year foxes also received a number tattooed into their ear. During the second year all of the animals caught were killed.

DESCRIPTION OF AREAS

The Panacea area is typical of the coastal strip in this region. Since the area is only one mile from the Ochlochnee Bay, the land rises only a few feet above sea level. It is a low rolling sandy region with lime sink ponds of various sizes and slow flowing streams. There is one large lime sink on the area called Otter Lake, a permanent cypress lake. The remainder of the lime sink ponds are not very deep and are inclined toward rapid plant succession. Buckhorn Creek,

a tributary of the Ochlochnee River, bounds the western end of this study area. To the west of this creek are reed-covered mud flats cut by several channels of the Sopchoppy and Ochlochnee Rivers, an effective barrier for foxes. To the east of the area lies Oyster Bay and to the south lies Ochlochnee Bay, both are also effective barriers. Any large amount of movement of foxes to or from the area must occur to the north. Within the fenced area of the refuge are



FIG. 1.—Facial characteristics of adult (above) and juvenile (below) gray foxes.

two large, formerly paved roads, numerous small sandy roads, section line clearings, and fire lanes resulting in unusual accessibility to every part of the study area.

The Norias and Sunnyhill Plantations are typical of the steeply rolling land of the Tallahassee red hills. They lie about 200 feet above sea level. Both areas have lime sinks but in contrast to the Panacea area, most of these were dry. No permanent streams flow on either area and the drainage pattern is erratic. The Norias Plantation sits on the northern end of Lake Miccosukee which is about 15 miles long and averages about a mile in width. Both plantations are surrounded by other smaller plantations and both have several unpaved county roads passing through them. Besides these roads many private agricultural roads cut between the fields. It was these agricultural roads that were used as trap lines for this study. The management of the plantations has a dual purpose, diversified farming and game management. The principle game species are the bob-white quail and wild turkey. Corn is the main crop planted on both plantations.

TABLE I.—Trapping results

	Panacea		Norias		Sunnyhill	
	1954	1955	1954	1955	1954	1955
Total Foxes	60	29	63	38	31	45
Adults	22	15	24	17	12	13
Juveniles	38	14	39	21	19	32
Total Male Foxes	30	14	31	20	16	27
Adults	11	9	13	12	6	8
Juveniles	19	5	18	8	10	19
Total Female Foxes	30	15	32	18	15	18
Adults	11	6	11	5	6	5
Juveniles	19	9	21	13	9	13
Sterilized Females Released	13	--	14	--	7*	--
Adults	6	--	5	--	3	--
Juveniles	7	--	9	--	4	--
Foxes Accidentally Killed	8	--	7	--	0	--
Males	3	--	2	--	0	--
Females	5	--	5	--	0	--
Foxes Released	54	--	56	--	31	--
Males	27	--	29	--	16	--
Females	27	--	27	--	15	--
Foxes Recaptured	15	7	7	7	5	2
Males	5	3	4	3	1	0
Females (intact and sterile)	10	4	3	4	4	2
Sterile Females	5	3	1	1	1	0
Foxes Re-released	13	--	7	--	5	--
Placental Scars	2,3,4,5	3,3	4,5,6,6	4,4,4	--	4,5,5
Trap Nights	3,038	3,182	4,435	4,744	2,387	3,475
Foxes Per Trap Night	.0197	.0091	.0142	.0080	.0129	.0129

* Laparotomy.

Prior to this study there had been essentially no trapping on the Panacea area since the incorporation of this area into the St. Marks National Wildlife Refuge in 1936. Trapping on the plantations prior to the advent of the fox investigations in 1952 was confined mainly to the tenant farmers and one of the supervisors who trapped for a bounty paid by the plantations. Before the beginning of this study 50 foxes were trapped by J. E. Wood in 1953 on the Norias Plantation and 24 were trapped on the Sunnyhill Plantation in the early spring of 1954.

RESULTS

The numerical results of the trapping are listed in Table I. There was an indication of trap avoidance by the male foxes. Since this avoidance factor was only one of the possible reasons for the difference between recapture rates of intact females and males (for instance, the difference might possibly have been due to excess mortality or emigration of males), the factor was called "absence of males" in the analysis of the data. The data also gave indications of the extent of the mortality of the female foxes due to the sterilization operation.

In an effort to determine the extent of mortality of the sterilized females and as a practice in developing the surgical technique, eight female foxes (from other areas) were hysterectomized. These eight foxes were then retained in cages to determine the outcome of the operation. All of these foxes survived. In February, eight months after the operation, these foxes were again opened up, their ovaries removed, and the success of the hysterectomy determined; the uterine horns were well healed and discontinuous. None of these foxes could have been successfully fertilized.

On September 4, 1954, an adult, apparently female fox weighing 11 pounds was caught in the central area of the Norias Plantation. According to the tooth wear, this fox was 17 months old. When the hysterectomy was performed, the fox was discovered to be a probable transverse hermaphrodite with underdeveloped, undescended testes. Because this fox was not a part of the breeding population of the Norias Plantation it was not used in the calculation of the population by the age-ratio-reduction method.

ANALYSIS OF DATA

Panacea Area

The number of foxes present on the Panacea area in 1954 has been calculated from the data in Tables I, II, and IV. The formula derived declares that:

$$\frac{\text{number of females sterilized}}{\text{reduction in the age ratio from the first to the second observation}} : \frac{(X) \text{ the total females in the population}}{\text{a total reduction of the age ratio to zero}}$$

These calculations give an estimate of 66 foxes. The following outline gives the steps for this estimate.

A. *Basic Information*.—In 1954 there were 38 juvenile and 22 adult foxes captured; giving a ratio of 1.73 juveniles to every adult. Eighteen of these foxes were females that were fixed (sterile or dead). In 1955, 14 juvenile and 15 adult foxes were captured; a reduction in the age ratio to 0.94 juveniles to each adult.

B. *Calculations*:

1. a change from 1.73 to 0.94 was a reduction of 0.79

$$\begin{array}{rcl} 2. & 18 & X \\ \hline & 0.79 & : \quad \frac{X}{1.73} \end{array}$$

3. $X = 39$ female foxes

4. $2X = 78$ foxes in 1954
or 1955 adjusted for absence of adults:

$$\frac{14 \text{ juveniles}}{18 \text{ adults}} = \text{ratio of } 0.78$$

then

1. a reduction of 0.95

$$\begin{array}{rcl} 2. & 18 & X \\ \hline & 0.95 & : \quad \frac{X}{1.73} \end{array}$$

3. $X = 33$ female foxes

4. $2X = 66$ foxes in 1954

In explanation of the above outline, the 5 dead females (accidental deaths from various causes, Table I) were included in the fixed female category because they too, were removed from breeding. The adjustment for the absence of adults is made because it was noted that a recapture rate of 19 per cent (all areas combined, Table II) was made for the intact (unsterilized females, but the recapture rate for the treated females was only 13 per cent (Table II). This difference was attributed to some effect of the surgical operation. However, the death or absence of these females did not affect their influence in changing the age ratio of the population, but it did have an effect on the number of adults expected to be captured in 1955. The 10 per cent recapture rate of male foxes also affected the number of adults captured in 1955. The difference in the males was attributed to either trap avoidance, or mortality, or both. Therefore a sufficient number of adult foxes were hypothetically added to the 1955 data to bring the total up to the 19 per cent recapture rate of the intact females. This amounted to 3 foxes for the

Panacea area and resulted in a difference of 12 foxes between the unadjusted and the adjusted population estimates. The intact females must also have experienced some mortality and learned to avoid traps to a degree. Thus, these adjustments are minimum ones for disturbances wrought by the trapping procedure and must have exceeded the three foxes added.

The recapture method may be compared with the age-ratio-reduction method as follows:

1954, released 52 marked foxes

1955, 15 adult foxes were caught, 7 of these were recaptures

$$\frac{7}{15} : \frac{52}{N}$$

$N = 111$ foxes in 1954 (unadjusted)

However, this figure is still unadjusted for the absence of some adults as described in the previous method. To adjust for these adults in this method, it is assumed that these adults were marked

TABLE II.—Release and recapture results of gray foxes within 1954

	Males		Intact females		Sterilized females	
	Re-leased	Recap-tured	Re-leased	Recap-tured	Re-leased	Recap-tured
Panacea	27	5	15	5	10	5
Norias	30	4	16	2	13	1
Sunnyhill	15	1	11	4	4*	1
Total	72	10	42	11	27	7
Per Cent						
Recaptured	13.9		26.2		25.9	
* Laparotomy						
1954 to 1955						
	Males		Intact females		Sterilized females	
	Re-leased	Recap-tured	Re-leased	Recap-tured	Re-leased	Recap-tured
Panacea	27	3	13	1	12	3
Norias	30	4	15	4	14	1
Sunnyhill	15	0	9	2	6*	0
Total	72	7	37	7	32	4
Per Cent						
Recaptured	9.7		18.9		12.5	
* Laparotomy						

animals (otherwise their absence would have been undetectable).
Thus, hypothetically:

1955, 18 adult foxes were caught, 10 of these were recaptures

$$\frac{10}{18} : \frac{52}{N}$$

$N = 94$ adult foxes in 1954 (adjusted)

The Schnabel (1938) method, a refinement of the recapture method adapted to continuous trapping over a period of time, may be applied to the data from the Panacea area. In this case the Schnabel method is not a refinement of the recapture method already presented, because that method was concerned with recaptures from 1954 to 1955. The Schnabel method which follows for the Panacea data is concerned only with releases and recaptures within 1954, and the results are therefore independent of the recapture method already described.

Schnabel Method:

Time Period	Number Caught A	Marked Caught C	Marked at large		AB	AD
			Unadjusted for Mortality B	Adjusted for Mortality D		
Aug. 17-24	35	0	0	0	0	0
Sept. 20-25	6	3	35	33	210	198
Nov. 22-30	19	6	41	35	780	665
Dec. 1-18	11	4	60	54	660	595
Totals		13			1650	1458

$$N = \frac{\Sigma(AB)}{\Sigma C} = \frac{1650}{13}$$

$N = 127$ foxes in 1954 (unadjusted)

or

$$N = \frac{\Sigma(AD)}{\Sigma C} = \frac{1458}{13}$$

$N = 112$ foxes in 1954 (adjusted for mortality during trapping)

Column D in the method shows the adjustment for mortality of the marked foxes during the trapping. The adjustment made was based on the assumed constant 0.64 annual probability of dying (Table III).

It is also possible to adjust this method for the absence of some foxes due probably to trap avoidance. However, the recapture rate applied is that for 1954 intact females which was 26 per cent as opposed to the 19 per cent recapture rate of intact female foxes a year later (Table II). The resulting three extra foxes were added to the last line of the captures in the outline of the method. The adjusted results are as follows:

$$N = \frac{\Sigma(AB)}{\Sigma C} = \frac{1830}{16}$$

$N = 114$ foxes (adjusted for trap avoidance only)

The combined adjustment for trap avoidance and mortality during the trapping gave an estimate of 101 foxes for the Panacea area in 1954.

On this area, due to the large capture of foxes (37) the first week of trapping in 1954, it was possible to apply the recapture method in three different ways. The number of captured and released foxes

TABLE III.—Age groups and mortality of the gray fox

Age	Number of foxes		Annual probability of dying		
	1954	1955	Within 1954 ¹	1954-55 ²	Within 1955
Panacea Area					
7 months	38	14	.63	.66	.. ³
19 months	14	13	.64	.78	.77
31 months	5	3	.60	1.00	1.00
43 or more months	2	0	1.00	1.00	..
Norias Plantation					
7 months	39	21	.69	.69	.. ³
19 months	12	12	.43	.75	.75
31 months	7	3	.71	.71	.33
43 months	2	2	0.00	1.00	1.00
55 or more months	2	0	1.00	1.00	..
Sunnyhill Plantation					
7 months	19	31	.63	.63	.72
19 months	7	7	.57	.71	.71
31 months	3	2	.33	0.00	0.00
43 or more months	2	3	1.00	1.00	1.00

¹ This probability of dying is calculated from the difference in size of of the age classes in 1954. It assumes that birth and death rates were constant for each age class for 1951, 1952, 1953, and 1954.

² This probability of dying is calculated from the difference in size of a group of siblings from 1954 to 1955. It assumes that the same proportion of the total population was caught both years.

³ This figure was not entered because it was altered from the normal by the sterilization of female foxes in 1954.

of the first week was compared with the number of captures and recaptures of the 2nd week, the 3rd week, and the 2nd and 3rd weeks combined. If the comparison is made with the 2nd week, the population estimate is 66 foxes in 1954. If the comparison is made with the 3rd week, the estimate is 104 foxes, and if the comparison is made with both weeks combined, the estimate is 92 foxes.

The removal method can be applied to the Panacea data because of the large catch made on the initial week of trapping. For data of this type the number of trappable foxes in 1954 may be visually estimated at about 70 (Fig. 2).

Norias Plantation

The population estimate of the Norias Plantation by the age-ratio-reduction method was 62 foxes for 1954. The adjustment for the absence of adults amounted to only 2 foxes. An adjustment for an increase in young was made, based on the fact that the reference

FOXES

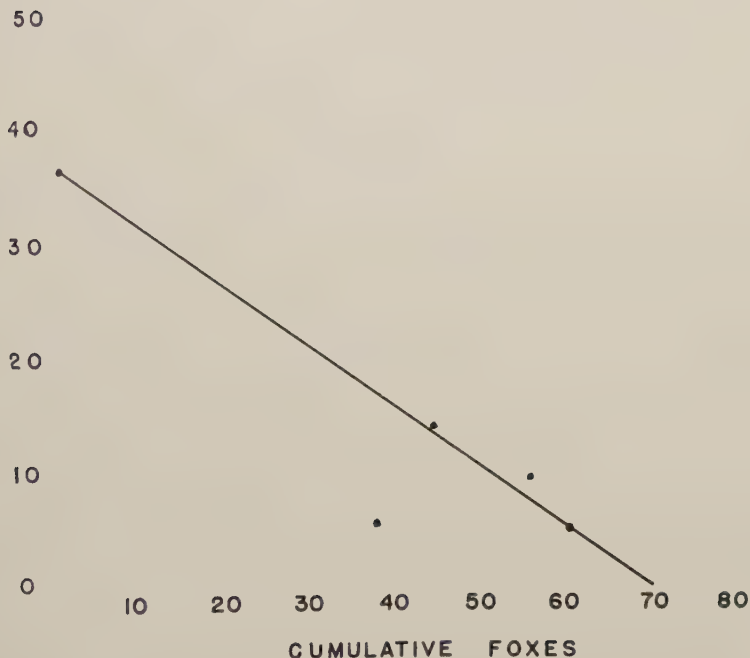


Fig. 2.—The removal method of estimate of population at Panacea. The ordinate gives the weekly catch of foxes. The abscissa gives the cumulative total.

area, the Sunnyhill Plantation, experienced a 0.40 increase in young (adjusted for trap avoidance) in 1955 over the 1954 figure. Since this area is adjacent to the Norias Plantation and the proportion of juveniles was nearly the same for both areas in 1954 (61% Sunnyhill and 63% Norias), it was felt necessary to apply this increase to the Norias population (see assumption 4).

By the recapture method, the unadjusted estimate was 136 foxes on the Norias area in 1954. When adjusted for the absence of adults, the estimate was 118 foxes.

The estimate obtained by the Schnabel method was 161 foxes, or 155 foxes when adjusted for mortality during trapping. When adjusted for the absence of adults, the estimate was 118 foxes, and with both of the above adjustments combined, the estimate was 100 foxes for the Norias area in 1954 by the Schnabel method.

Sunnyhill Plantation

Because the Sunnyhill Plantation served as the reference area for the study, there can be no calculations of the population by the age-ratio-reduction method. However, the recapture method gave an estimate of 202 foxes (unadjusted), or 99 foxes when adjusted for the absence of adults. According to the Schnabel method, the estimate was 75 foxes (unadjusted), or 71 foxes when adjusted for mortality during trapping, or 56 foxes when adjusted for trap avoidance. The combined adjustments for the Schnabel method estimated 54 foxes on the Sunnyhill area for 1954.

DISCUSSION

Panacea Area

The estimates of the various methods for determining the size of the same population ranged from 66 to 127 foxes. Many of the observed differences were probably due to trap avoidance (which could not be completely adjusted for) on the part of the foxes. Because it is more greatly affected by this factor, the recapture method gave consistently higher estimates than did the age-ratio-reduction method. The removal method gave essentially the same answer as the age-ratio-reduction method, indicating that in 1954, nearly all of the foxes were trappable on the Panacea area. Using the age-ratio-reduction method, the density of the foxes was about 4 per square mile. Conceivably, the area influenced by the trapping was greater than the 16 square miles trapped. Foxes that have an average home range diameter of about 2 miles, would be expected to range into the study area from outside.

Norias Plantation

On the Norias Plantation the recapture method again gave an estimate higher than that of the age-ratio-reduction method. The removal method and the recapture method applied within 1954 on the Panacea area, were not usable for the Norias area because there was no large initial catch of foxes during the first week of trapping.

The previous trapping experience of the foxes on the plantation areas probably accounts for their wariness as compared with the fox population on the Panacea Unit of the St. Marks National Wildlife Refuge. On the basis of 62 foxes estimated for the Norias area by the age-ratio-reduction method, the density of foxes was about 3 per square mile.

Sunnyhill Plantation

The fox population on the Sunnyhill area was expected to be nearly the same as that on the Norias Plantation. Yet the estimates for the Sunnyhill Plantation were considerably lower (comparing the same methods) than those for the Norias Plantation. The difference in size of these populations may be readily explained by the fact that 24 foxes were removed from the Sunnyhill area in March and April of 1954 by J. E. Wood for another phase of the over-all fox study (Wood; 1954, 1955, 1958, 1959). If these foxes and their expected progeny, minus a mortality of 0.30 for one half a year, were still at large on the plantation when the study commenced in June of 1954, they would add 44 foxes to the population bringing it up to a figure comparable to the estimates made for the Norias Plantation by the recapture method.

DISCUSSION OF ASSUMPTIONS

Having arrived at estimates for the sizes of the populations, it becomes desirable to examine the assumptions made in these methods in the light of the efforts made to check them.

(1) The sterilization is complete.

This assumption is probably entirely correct because every one of the 8 caged animals and all 11 of the recaptured females that had been sterilized showed complete and apparently permanent separation of the reproductive tract.

(2) The sex and age ratios in the sample are representative of the actual sex and age ratios.

This assumption is probably nearly correct since ratios obtained by Wood (1954, 1955, 1958, 1959) in the same region compare favorably with those obtained by this study. In support of the surmise that there is no tendency for one of the age or sex classifications to be caught more easily than others, is the observation that the sex ratios in all cases (except the reference area in 1955) are very close to the expected 50-50 ratio and the age groups are likewise close to the expected values. The juvenile ratio never exceeded the average number of young as determined from the reproductive tracts (Wood, 1955).

(3) There is no immigration or emigration of foxes to or from the study areas.

The mile wide peripheral area around the 6 square mile central area wherein the females were sterilized was designed to check this assumption. Also natural barriers of water were used whenever possible to minimize movement. As a further check on the movement of foxes out of the areas, other members of the over-all fox study trapped the

smaller plantations around the Norias and Sunnyside plantations for a distance of 15 miles. The tags in the foxes' ears contained a return address to further aid the possibility of recovery. The recaptures indicated that the average home range of the gray fox in this region was probably about 2 miles in diameter or a little more than 3 square miles in area.

In reference to emigration, two foxes were recaptured outside the study areas. One of these was caught 11 miles from its first capture. The other fox was caught three and three-quarters miles from its first capture, but only one-quarter mile from the outside boundary of the peripheral area. There was no check on the immigration other than that from the peripheral to the central area. Only one fox shifted in this direction while 3 shifted from the central to the peripheral area. Most of the shifting of ranges occurred between December and March. The following discussion of assumption 4 indicates that some movement probably did occur on the Norias Plantation (and if so, probably on the Panacea area too, but to a lesser degree because of natural barriers). However, the analysis of the data does not produce an unreasonably high estimate (which it would if many of the sterile females emigrated) and thus most of this movement probably occurred between the peripheral area and the surrounding relatively lightly trapped region. These females would then have had an effect on the lowered juvenile ratio of the study area due simply to their proximity. Movement apparently did not seriously affect the results of the method.

(4) That the reproductive rate and the probability of dying remain constant during the study.

There was no way to check directly the mortality of the foxes. There was indication that at least on the reference area, either the reproductive rate jumped above the average for the region (4.48) to 6.40 young per female, or the trap avoidance by the adults caused this apparent increase. The recapture rate in the reference area the second year was remarkably low (Table II). However, even when the data were adjusted for trap avoidance as previously discussed, there was still an increase of 0.4 juveniles per adult on this area due either to increased reproduction or trap avoidance of adults. The adjustment made for this factor in calculating the size of the Norias fox population was labeled "increase in young," to distinguish it from the previous adjustment for trap avoidance. Perhaps, if the reproductive rate was stable, this adjustment was then an additional check on trap avoidance which may have accounted for all trap avoidance. However, when this factor ("increase in young") was introduced into the calculations of the size of the Norias fox population, the resultant answer indicated that all foxes were caught in 1954. If all foxes were caught in 1954, and no movement occurred into the area, then all adults captured in 1955 should have been marked (providing there was no loss of ear tags). But there were ten unmarked adults captured on the Norias Plantation in 1955. Although there was no loss

of marking within the first year, there was a 33 per cent loss of ear tags in these foxes from 1954 to 1955 (Lord, 1956). This could account for five or six of the unmarked foxes, but the remaining four or five unmarked adult foxes must either have avoided the traps in 1954 or moved into the area during the nontrapping interim between 1954 and 1955. If the former was the case, then providing for mortality, 14 foxes were left untrapped in 1954. But the adjustment for "increase in young" contradicts this, claiming no foxes were left untrapped in 1954. Clearly, one or the other or both of these views are wrong. In contrast, if the latter assumption is used, that the unmarked foxes were immigrants, then for a valid calculation of the populations the amount of adult, marked fox emigration must have been equal to this immigration. Probably both trap avoidance and movement were involved.

(5) There was no loss of marking on the foxes for the first year.

The ear tags used were designed for the purpose and were reasonably successful. If they failed most foxes retained some sort of scar on the foot, or in the ear where the tag pulled out, at least for the first year. After the tattoo kit was obtained all foxes were permanently marked.

(6) The relative trapability of the young and adults does not change during the time of the study.

In reference to the previously untrapped foxes this assumption is probably true. However, a fox that has once been caught will probably learn to some degree to avoid traps. Yet 28 foxes were recaptured within the first year of the study. Within 1954, 20 per cent of the foxes were recaptured. Within 1955, 13 per cent were recaptured. According to the average probability of survival (0.36) and expecting the 1954 recapture rate to occur again in 1955, the recapture rate of 1955 should have been only seven per cent. The difference between the expected (7%) and the actual (13%) proportion of recaptures for 1955 may be that some of the foxes forgot their former trap experience during the seven months interim between the 1954 and 1955 trapping periods. Still, some foxes avoided traps. Avoidance was readily apparent in the field where the tracks of foxes in the sandy soil showed that they were not caught even though being attracted by the scent. The figures comparing the proportion of the recaptures of the males and the intact females also indicated trap avoidance by the males.

(7) There is no marked change in the behavior of the sterilized females.

The scope of this study made it impossible to carry out a behavioral or physiological check on this assumption. The eight caged, sterilized females showed no obvious difference in behavior. On the Norias Plantation, a male and female remained paired although shifting their range after the female was hysterectomized. On the basis of what is known of the physiology of the canine uterus (Reynolds, 1949) it is possible to surmise that there were no physio-

logical changes in the sterilized foxes due to the hysterectomy.

(8) That no other factor such as climate, changes enough during the study to affect the age ratio.

Actually, although the weather data showed no marked changes during the time of the study, so little is known of the effect of climate on fox populations that some unsuspected, apparently minor change, might seriously affect the population.

(9) The observed reduction in the ratio of juveniles to adults from the first year to the second year was due to the sterilization of the female foxes.

This assumption is basic to the method and no other cause for a reduction of this ratio other than chance appears plausible.

CONFIDENCE LIMITS

Professor W. G. Cochran, Bio-statistics Department, Johns Hopkins University, provided the following description for determining the confidence limits for the age-ratio-reduction method for estimating populations.

"The error in the estimated total population arose from several sources: (1) any incorrectness in the biological assumptions on which the method is based, (2) sampling errors in the estimated ratio of juveniles to adults in the two years, (3) errors in the adjustments made to the number of adults in the second year on account of decreased trapability. Quantitative assessment of the degree of error from source (1) is difficult and requires special studies, this being true also of the marking and recapture methods. It is possible to give an approximate formula for the error due to source (2), as follows.

The unadjusted estimate of total population is

$$\hat{N} = \frac{2f_s \frac{p_1}{q_1}}{\frac{p_1}{q_1} - \frac{p_2}{q_2}}$$

where

f_s = number of sterilized females.

p_1 = proportion of juveniles in the 1st year. $q = 1 - p$

p_2 = proportion of juveniles in the 2nd year. $q = 1 - p$

The approximate coefficient of variation of N (i.e., ratio of the standard error to the mean) is

$$\frac{(\hat{F} - f_s)}{f_s} \sqrt{\frac{(1 - r_1)}{n_1 p_1 q_1} + \frac{(1 - r_2)}{n_2 p_2 q_2}}$$

where

$$\hat{F} = \frac{\hat{N}}{2} = \text{estimated female population.}$$

n_1 = size of sample in first year.

r_1 = trapping success (proportion of total foxes captured) in the first year.

n_2, r_2 have the same meanings for the second year.

The standard error becomes low when the samples are large

(n_1, n_2 large) or when the trapping success is high (r_1, r_2 near 1).

Sampling errors in the adjustments mentioned in (3) above will increase the standard error to some extent, so that this formula can be regarded only as indicating the *maximum* precision which the method can achieve. For computation purposes the formula can be rewritten

$$\frac{SE(\hat{N})}{\hat{N}} = \frac{(\hat{F} - f_s)}{f_s} \sqrt{\frac{n_1(1 - r_1)}{a_1 j_1} + \frac{N_2(1 - r_2)}{a_2 j_2}}$$

where a, j are the numbers of adults and juveniles.

Applying this formula to the adjusted Panacea data,

$$\frac{SE(\hat{N})}{\hat{N}} = \frac{(33 - 18)}{18} \sqrt{\frac{(60)}{(38)(22)}(.09) + \frac{(32)}{(18)(14)}(.32)} \quad (.32)$$

The minimum standard error is about 18%.

The approximation formula becomes suspect when the standard error becomes high, say over 30%.

Applying the formula to the adjusted Norias data;

$$\frac{SE(\hat{N})}{\hat{N}} = \frac{(31 - 18)}{18} \sqrt{\frac{(63)}{(39)(23)}(.00) + \frac{(40)}{(21)(19)}(.22)} \quad (.22)$$

The minimum standard error is about 22 per cent.

REPRODUCTION AND MORTALITY

In northern Florida the birth of the majority of young gray foxes is in March (Wood, 1958), about a month ahead of northern United States. Gray foxes are suspected of being monogamous at least for the year (Seton, 1909). In support of the monogamy statement, a pair of probably sibling foxes changed their range from one year to the next. The female fox had been sterilized. This means that in all probability these two foxes remained paired through a mating season

and denning season, at least until the advent of a new mating season, and in spite of a change in home range and an unsuccessful mating insofar as producing a litter was concerned. Incidentally, this case supports the assumption that there was no change in the behavior of sterilized females, for she apparently remained sexually attractive to her mate after the operation.

An average placental scar and embryo count compiled by Wood (1958), gave 4.56 as the average number of embryos per female in southern Georgia and northern Florida. The mean number of placental scars of foxes from the Norias and Sunnyhill plantations was 4.71. The mean number of placental scars in six females from the Panacea area, however, was only 3.33.

If it is assumed that the fox populations investigated in this study were stationary, that is, for each year the number born were equal to the number that died, and immigration was negligible or balanced by emigration, then we may determine the annual probability of dying for these populations.

On the Panacea area the ratio of juveniles to adults was 64 per cent. The average age of these juveniles was 7 months. Assuming a stationary population, the annual probability of dying of adult foxes was 0.64. Using the figure of 4.56 as the average number of young per female (Wood, 1958), the young then make up 69 per cent of the fox population. Again assuming a stationary population, and a constant adult mortality throughout the year, the probability of dying for juvenile foxes from uterus to trapability (average of 7 months) was 0.43. This probability of dying is low compared to other species and indicates that the care of the young by the adults is successful. By assuming a stationary population it is possible to calculate that the average longevity or life expectancy of a fox that reaches 7 months of age was about 18.5 months in this natural fox population.

The tooth wear system developed by Wood (1958) was applicable to the foxes of the Panacea area. The number of foxes in each age class, assuming a constant birth rate over the past years, and a constant death rate for each age group, is a result of the death rate for its age group. Table III shows the number of foxes in each age category for both years of the study, and their annual probability of dying.

The annual probability of dying was calculated for the Norias Plantation to be 0.63 for adult foxes and 0.43 for juveniles. The number of foxes in each age class and their annual probability of dying is listed in Table III. The average longevity of adult foxes on the Norias Plantation was 1.59 years or 19 months.

On the Sunnyhill Plantation the annual probability of dying of the foxes was similar to that of the Norias Plantation, being 0.61 for adult foxes and 0.47 for juveniles. Table III lists the numbers of foxes in each age class and their annual probability of dying for this plantation. The average longevity for adult foxes on the Sunnyhill Plantation was about 19.7 months.

HOME RANGE AND FAMILY AGGREGATIONS

The home range is that area occupied continuously by the fox for most of the year. Somewhat more extensive traveling occurs when the mating urge stirs them (Sheldon, 1950; Layne, 1956), but from the time they pair off until the next mating season approaches, the foxes confine themselves to their home range. The family aggregation is self explanatory and is distinguishable on an area because of its isolation from other families and foxes.

Probably the distance between captures and recaptures of the foxes and the diameters of the family aggregations gives a clue to the approximate size of the home range of the gray fox. Of the 141 foxes trapped and released on the three study areas, 28 were recaptured and released during the first year, and 18 were recaptured during the second year. It is apparent that the chance of getting recapture distances extending across the complete diameter of the home range of an individual fox is small. Conversely, the number of recaptures around the center of the home range should be most numerous. Table IV illustrates that the field data agree with this concept. The reason that no recaptures were made at the point of the first capture was due to the trapping procedure (seldom was a trap placed in the same place twice). The data indicate that the probable maximum diameter for the home range of the gray fox in this region was about two and one-half miles and the average was about two miles. The two foxes recaptured in 1955, three and three-quarters miles

TABLE IV.—Recapture distance and family aggregation diameters

Distances in miles	Number of recaptures		Number of family aggregations 1954 & 1955
	within 1954	from 1954 to 1955	
.00- .25	6	2	1
.26- .50	4	4	8
.51- .75	5	1	6
.76-1.00	4	0	4
1.01-1.25	5	1	1
1.26-1.50	0	3	1
1.51-1.75	2	4	0
1.76-2.00	1	0	0
2.01-2.25	0	0	0
2.26-2.50	1	0	0
2.51-2.75	0	0	0
2.76-3.00	0	0	0
3.01-3.25	0	0	0
3.26-3.50	0	0	0
3.51-3.75	0	2	0
3.76-4.00	0	0	0
11 miles	0	1	0
Total	28	18	21

from their 1954 point of capture possibly represents a shift in home range. In fact the 1955 data also probably show a slight shift in home range of about one half of the foxes. It is possible that a winter shuffle, as described by many writers, (e.g., Layne and McKean, 1956), resulted in a rematching of many pairs with their close neighbors and the dominant individual of the new pair pulled its new mate into its home range.

The family aggregation as used within this paper is a cluster of individuals within a small area as plotted on the map and probably represents members of a family unit. It was noticed during the trapping, that in some areas a number of foxes would be caught close to one another, and the group consisted of an adult male and female and a number of juvenile foxes. This group might be isolated from the nearest captured fox by as much as one mile. Consequently all the captures for both 1954 and 1955 were plotted on separate maps and designated as to age and sex of the fox. Twenty-one family aggregations could thus be reasonably well designated and several others might also have been added. The maximum diameters of these family aggregations are listed in Table IV. It can be seen that these data are also in support of the estimate arrived at for the home range of the gray fox based on recapture distances. Family aggregations caught in the summer were tighter in their grouping than those caught in the fall. Many of the scattered juveniles were caught late

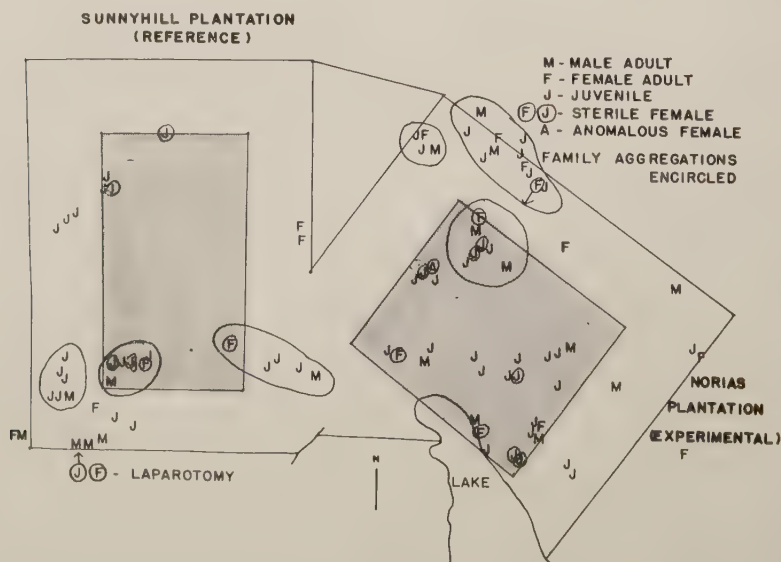


Fig. 3.—The distribution of the capture of foxes in 1954 on the Norias and Sunnyhill Plantations.

in the trapping period, and possibly represent the beginning of dispersal from the family unit. The average maximum diameter of the family aggregations was 0.74 miles. The relatively long duration of the maintenance of the family aggregation as a unit probably accounts for the low mortality of the juvenile foxes.

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The Diel Cycle of Stratification and Productivity in Two Lakes of the Chuska Mountains, New Mexico¹

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ABSTRACT: Deadman and Whiskey lakes are shallow lakes having abundant rooted vegetation. They are located on the flat, rolling crest of the Chuska Mountains. The vertical plant stems and thermal density strata inhibited turbulence in the water columns of these lakes so that a discrete trophogenic zone developed each day during photosynthesis. This stratification was disrupted by descending density currents when the surface water was cooled each evening.

Because the daily stratification inhibits chemical interchange between the trophogenic zone and the tropholytic zone adjacent to the sediments, the rate of net productivity can be estimated from measurements of the diurnal accumulation of oxygen in the trophogenic zone. The mean rate of net oxygen production derived from three 20-hour studies of the cycle of stratification was $364 \text{ mg/m}^2/\text{hr}$, indicating that the net productivity among the rooted plants in these lakes is on the order of $1 \text{ g carbon/m}^2/\text{day}$.

INTRODUCTION

The lakes scattered along the flat top of the Chuska Mountains are characteristically shallow and have an abundance of rooted aquatic vegetation. Three 20-hour series of observations were completed on Deadman Lake and Whiskey Lake, two of the largest of these lakes, during July and August, 1959. The studies revealed that very large thermal and chemical changes occurred regularly each day among the plants. Furthermore, these changes were associated with a diel cycle of thermal stratification.

Diel chemical changes are not only ecologically significant; they are also valuable indexes of productivity. Several papers have appeared recently (Jackson and McFadden, 1954; Odum, 1956; Verduin, 1956; Talling, 1957) in which daily fluctuations of oxygen and carbon dioxide have been utilized to evaluate the productivity *in situ* of natural waters. This approach to the study of productivity usually has been applied to phytoplankton communities, because the lower limit of the trophogenic zone among rooted aquatic plants often is difficult to identify. In Deadman and Whiskey lakes, however, the chemical changes associated with photosynthesis were observed to be

¹ Contribution No. 703 from the Department of Zoology, Indiana University. This is one aspect of an investigation of the sedimentational and developmental history of the Chuska Mountain lakes, a study directed by Dr. Herbert E. Wright, University of Minnesota. The writer expresses his gratitude to Dr. Wright and Dr. David G. Frey, Indiana University, for financial support from their National Science Foundation Grants, G-5655 and G-6157. The writer is also grateful to Dr. Frey for advice and criticism during the preparation of the manuscript. The author wishes to thank his wife, Roberta, and Richard F. Wright for their assistance in the field and laboratory.

confined within a surficial zone by the daily development of thermal stratification. Hence, oxygen fluctuations, although perhaps not carbon dioxide fluctuations, can also be used to estimate the productivity of these communities.

The Chuska Mountains, extending NNW for 95 km across the northern part of the Arizona-New Mexico border, are the major upland (elevation 2,700 to 3,000 m) on the Navajo Indian Reservation. The top of the range forms a relatively flat, rolling crest which in places is 2 to 5 km wide. The eastern edge of the crest is an abrupt escarpment from which the relatively undissected mountain-side slopes down to the Chaco Valley, more than 1,000 m below. On the west, the crest gives way to numerous canyons that lead down to the Defiance Plateau. Vegetational cover on most of the summit consists of an open ponderosa pine (*Pinus ponderosa*) forest that grades into stands of Douglas fir (*Pseudotsuga taxifolia*), blue spruce (*Picea pungens*), and subalpine fir (*Abies lasiocarpa*) along the north-facing slopes of the canyons. Below 2,400 m the ponderosa pine is replaced by the pinyon-juniper association. The range is capped by Chuska sandstone (Wright, 1956) which is pitted with hundreds of small basins, many of which contain water permanently, others only tem-

TABLE I.—Chemical analyses of waters from the Chuska Mountains (these analyses were performed by the U. S. Geological Survey Laboratory in Denver, Colorado, on water samples submitted by Dr. H. E. Wright; all values are in ppm unless otherwise indicated)

	Long Lake	Wide Lake	Basalt Lake	Boot Lake	Deadman Lake	Landslide Lake	Owl Spring
SiO ₂	4.2	4.2	2.4	1.8	7.6	0.6	35.0
Al	0.1	0.2	0.5	0.6	0.3	0.3	
Fe	0.1	0.2	0.3	1.5	0.1	0.3	
Mn	0.0	0.0	0.0	0.0	0.0	0.2	
Ca	19.0	9.6	24.0	29.0	17.0	11.0	60.0
Mg	4.4	2.9	9.7	6.8	3.9	1.9	11.0
Na	7.4	3.8	2.8	5.5	3.5	2.2	4.8
K	1.4	3.2	3.0	2.2	2.6	3.2	
HCO ₃	54.0	42.2	127.0	119.0	22.0	42.0	226.0
CO ₃	10.0	0.0	0.0	0.0	26.0	0.0	0.0
SO ₄	21.0	2.6	0.9	0.4	4.4	0.9	5.4
Cl	1.0	7.0	2.0	5.0	2.0	6.0	8.0
F	0.0	0.3	0.2	0.0	0.3	0.0	0.0
NO ₃	0.0	0.0	0.0	0.0	0.0	0.0	0.5
PO ₄	0.0	0.1	0.6	0.2	0.0	0.5	
TDS 180°	91.0	77.0	108.0		104.0	74.0	
TDS Sum	94.0	55.0	107.0	110.0	77.0	47.0	231.0
Hardness as CaCO ₃	66.0	36.0	100.0	100.0	58.0	35.0	194.0
pH	9.0	6.8	7.0	6.9	9.9	6.5	

porarily after periods of high precipitation. Chemical analyses from a number of lakes and springs in the region (Table I) show that these are carbonate-bicarbonate waters rather than saline, even though the lakes occupy closed basins and are rarely drained.

DEADMAN AND WHISKEY LAKES

Deadman and Whiskey lakes are two of the largest and most nearly permanent lakes in the Chuska Mountains. Deadman Lake (elevation 2,780 m) is located about 5 km west of Toadlena, New Mexico, equidistant from either end of the range and about 0.5 km from the eastern escarpment. The lake is roughly rectangular, about 380 m long and 300 m wide, with an area of 11 ha and an average depth of 0.6 m during the summer of 1959. The maximum depth recorded in 1958 was 1.25 m, but in July, 1959, the maximum depth was 0.8 m. There is no record that Deadman Lake has been recently dry. A mat of *Chara* 15 to 30 cm thick covered the bottom of the southern half of the lake, but the vegetation in the northern half comprised floating and emergent stands of *Elvcharis macrostachya*, *Myriophyllum exalbescentis*, and *Polygonum amphibium* with a *Chara* under-story.

Whiskey Lake (elevation 2,700 m) is located near the southern end of the Chuska Mountains, south of Washington Pass.² It is 850 m long, 250 m wide, with an area of 21 ha. The depth was 1.2 m during July and early August, 1959, but a maximum of 1.7 m was recorded in 1958. Although Whiskey Lake was dry in 1956, it filled to the level of its outlet in 1957. Bunches and beds of bullrush (*Scirpus acutus*) were scattered all over the lake except in a zone 8 to 10 m wide along its circumference. In this peripheral zone and in almost all of the rest of the lake there was a dense growth of *Polygonum amphibium* and *Myriophyllum exalbescentis*. Emergent or floating vegetation was absent in a few areas, but even these had a bottom mat of *Chara*.

Although horses and cattle were seen browsing in the lakes occasionally, and the Navajo allow their herds of sheep and goats to graze in the meadows around the lakes, the aquatic vegetation does not seem to have been damaged excessively. Larval and adult salamanders (*Ambystoma tigrinum*) were abundant in both lakes. Whiskey Lake was stocked with 16,000 rainbow trout fingerlings in May, 1958, and by August, 1959, many of these had grown to the rather extraordinary length of 30 cm.

² The lake discussed here is located on the Tohatchi quadrangle (1:62,500) published by the United States Geological Survey. An artificial lake located 10 km NW of Crystal, New Mexico, at the western base of the Chuska Mountains, is also called Whiskey Lake, according to the Shiprock, New Mexico-Arizona topographic sheet (1:250,000), but it is called Little White Cone Lake on the Sonsuela Buttes, Arizona-New Mexico quadrangle (1:62,500).

MATERIALS AND METHODS

A raft composed of two sheets of plywood lashed to four truck tire inner tubes served as a sampling platform. While collections were being made the fore and aft ends of the raft were firmly lashed to poles driven into the bottom. Since one of the poles extended about 1 m above the water surface, the collecting station could be located precisely and easily, even at night.

Water samples for the determination of oxygen, temperature, pH, and carbon dioxide were obtained with a modified Irwin Sampler (Welch, p. 204-206). This consisted of a one-liter reservoir bottle connected by rubber tubing to a series of two 250-ml sample bottles. Water was raised from the lake through an intake tube into the series of bottles by withdrawing air from the reservoir bottle with a small plunger-type bilge pump. In order to obtain water from specific depths, the free end of the intake tube was positioned at a point on a graduated iron rod, one end of the rod and the attached tubing were lowered through a slot in the center of the raft, and the end of the rod was pressed against the bottom while water was entering the intake tube. This collection technique permitted sampling the water column at any depth with minimal disturbance. The oxygen content of a stratum of water was determined from the water in the first sample bottle of the series, pH from the second, and temperature from the reservoir bottle.

The oxygen concentration was determined using the unmodified Winkler method. A Beckman model N pH meter was used to meas-

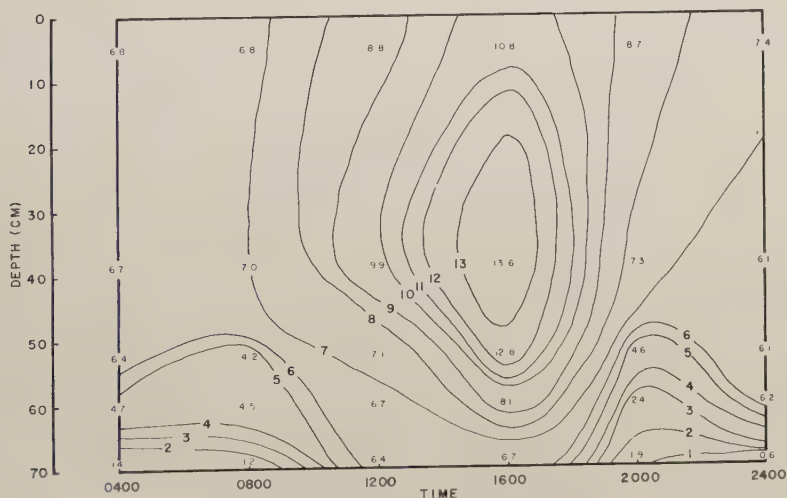


Fig. 1.—Time-depth diagram of oxygen distribution in Deadman Lake beginning at 0400 hours, July 13. The numbers in small type on the diagram represent the measured concentrations in ppm.

ure hydrogen ion concentration. Temperatures were measured with a simple mercury-bulb thermometer calibrated in degrees. A more precise means of determining temperatures would have been desirable, but fortunately thermal changes were so large that this thermometer was adequate to determine the course of thermal variations. Changes in carbon dioxide concentrations were determined from pH titration curves according to the method proposed by Verduin (1956), using $N/44 \text{ H}_2\text{SO}_4$ as the titrating agent. The carbon dioxide concentration was assumed to be equivalent to the volume of standard acid necessary to establish the pH in the water samples. The shortcomings of this technique of determining carbon dioxide among rooted aquatic plants will be discussed below.

RESULTS

The diel cycle of stratification among the plants of these lakes was first observed during 20-hour studies of oxygen fluctuations. The results of a study on Deadman Lake between 0400 hours and midnight, July 13, are shown in a time-depth diagram, Figure 1. The depth of the water was 68 cm. A vigorous growth of *Chara* occurred below 30 cm, and the stems of a few *Myriophyllum* plants extended up to the 20 cm depth.

In the morning, before 0800 hours, there was little stratification in the water above 50 cm. Oxygen was rather uniformly distributed, ranging from 6.4 to 6.8 ppm. At greater depths, between 50 and 68 cm, the oxygen concentration decreased rapidly to less than 1.4 ppm near the sediments, and the trend was toward oxygen depletion until 0800 hours.

Oxygen concentration increased at all depths after 0800 hours, and a distinct oxygen stratification developed by 1600 hours. Maximum oxygen content among the *Chara* was 13.6 ppm during stratification, and oxygen increased to 6.7 ppm even next to the bottom. The average oxygen increase between 0800 and 1600 hours was 6.0 ppm in the upper 60 cm of the water column.

A severe thunderstorm with strong gusts of wind occurred between 1600 and 2000 hours. By 2000 hours the stratification was deteriorating in the upper 50 cm, and the uniform oxygen distribution that occurred early the previous morning again prevailed by midnight. In the early evening the oxygen began to decrease at 50 and 60 cm, but before midnight there was a surprising oxygen increase in this stratum. It was largely this anomalous oxygen increase during the hours of darkness that indicated the desirability of more complete investigations including data on temperature, pH, and carbon dioxide.

THE RELATIONSHIP BETWEEN VEGETATION AND THE STRATIFICATION

A diel oxygen stratification of the type occurring in Deadman Lake might be expected in any stable body of shallow water where there is abundant photosynthesis each day. In order to determine if the stability and stratification in the water column could be attributed

to the rooted vegetation, vertical series of temperature, pH, and oxygen determinations were made in two areas of Whiskey Lake. One station, with an area of about 10 m², was free of rooted vegetation except for a bottom mat of *Chara* 10 to 15 cm thick; at the other area, a dense growth of *Myriophyllum* and *Polygonum* reached the surface. The depth was similar in both areas, 114 and 122 cm, respectively. The data were gathered between 1400 and 1600 hours, July 30, when the weather was clear and sunny, and the air temperature was 23° C.

The different conditions in the two areas are shown in Figure 2. Temperatures in the open water decreased from 23° at the surface to 22° at the bottom, and oxygen decreased gradually from 9.35 ppm at the surface to 6.58 ppm at the bottom. The pH of the water

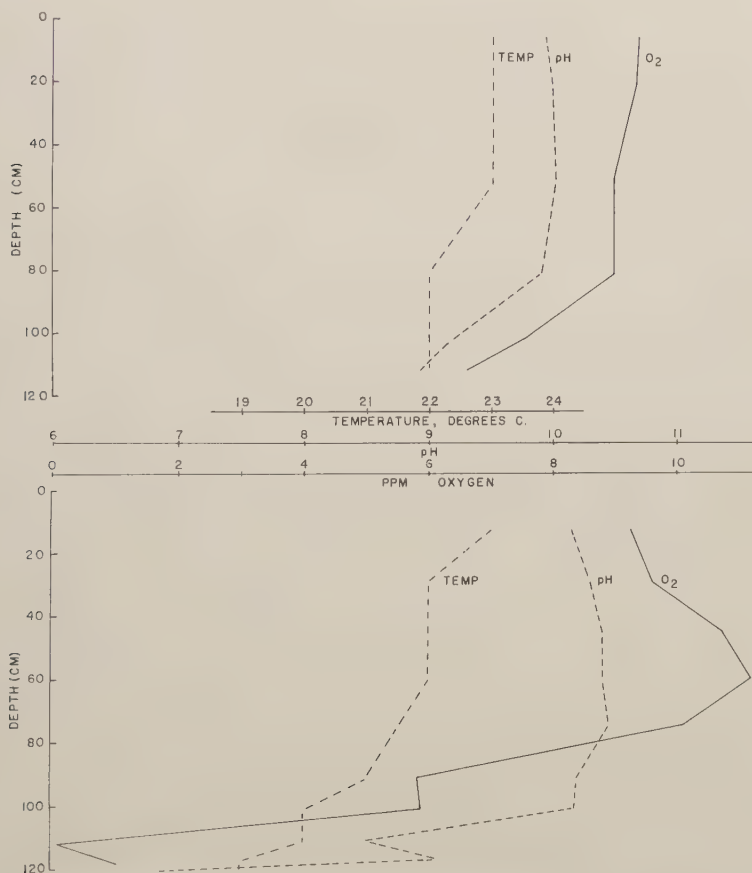


Fig. 2. Oxygen concentration, pH, and temperature in the open water (upper curves) and among the vegetation (lower curves) in Whiskey Lake between 1400 and 1600 hours, July 30.

column, however, was somewhat less regular. The pH was 9.92 at the surface, 10.01 at 51 cm, and 8.93 at the bottom.

The conditions among the plants were considerably different from conditions in the open water. The temperature data indicate a distinct thermal stratification. The surface water temperature was the same as the air temperature, 23° C, but the bottom water temperature was only 19°, 3° colder than the bottom temperature in the open water. There was also a definite oxygen stratification among the plants in which oxygen concentration varied between 8.81 ppm at the surface, 11.21 ppm at 60 cm, and 0.96 ppm at the bottom. All pH values in the upper 100 cm were greater than 10, with a maximum of 10.45 at 76 cm. The water became less alkaline at depths below 100 cm, with pH decreasing to 6.88 at the bottom.

These data from two areas in Whiskey Lake compare favorably with the results obtained by Buscemi (1958, Fig. 3) in Parvin Lake, Colorado. He found uniform oxygen distribution in the surficial meter of water, above a mat of *Elodea*. In the deeper water among the plants, between 1.2 and 2.2 m, oxygen was stratified as among the *Myriophyllum* and *Polygonum* in Whiskey Lake.

It is evident from the comparison of these two areas in Whiskey Lake that the stratification was a phenomenon associated with the rooted plants. Apparently the vegetation reduced the effects of the wind, inhibiting the lateral water movement and turbulence that would normally result from wind action. Consequently the limited circulation enabled thermal density strata to develop as the water absorbed solar radiation. These density strata, in turn, restricted vertical water movements. The inhibitors of turbulence—the vertical plant stems and horizontal density strata—enabled a thermal gradient of 4° to develop in the water column in mid-afternoon. Moreover, oxygen accumulated and pH became very alkaline in the strata where there was sufficient light for photosynthesis. Evidently the plants obtained carbon dioxide from bicarbonates, because free carbon dioxide could hardly exist at the alkaline pH observed in the region of photosynthesis.

Vaas and Sachlan (1955), who studied diurnal fluctuations in shallow fish ponds in Indonesia, measured daily temperature changes in a water-filled pit near their laboratory. The diameter of the pit was 2 m, and the depth was 2 m. The average of 30 series of temperature readings (their Table 1) showed that the water in the pit was homothermal at 0730 hours, but that there was a distinct thermal stratification by 1530 hours involving a thermal gradient of 4.9° in the surficial meter of water. The temperature at the bottom did not increase during this time period because of turbidity (Secchi disc reading = 80 cm). The authors concluded that "wind action is practically nil and absorption of sunlight is the principal source of heat."

The similarity between the thermal gradient among the water plants of Whiskey Lake and the gradient in the pit indicates that

turbulent heat transfer is inhibited as effectively by the vegetation as if the water column were bounded by walls like those of the pit.

DIEL CYCLE OF STRATIFICATION IN WHISKEY LAKE

A detailed 20-hour study of temperature, pH, dissolved oxygen, and carbon dioxide among the rooted plants in Whiskey Lake was made on August 2, 1959, to obtain more information about the diel cycle of stratification. Collections were made at 4-hour intervals between 0400 and 2400 hours at depths of 5, 30, 60, 90, 110, and 120 cm.

The temperature trends at 5, 60, and 120 cm are shown in Figure 3. At 0400 hours the lake was virtually homothermal with temperatures between 16.5° and 17.0° C at all depths. Subsequently, between sunrise (0537 hours) and 0800 hours, the entire water column warmed an average of 1.8°. Between 0800 and 1200 hours, however, the surface water was heated more rapidly than the lower depths, and thermal stratification developed. Since most of the temperature increase was in the upper 60 cm, and since air temperatures were lower than water temperatures during the warming phase, the temperature increase must have been caused by direct absorption of solar radiation rather than by contact with the atmosphere. After 1200 hours the surface water began to cool. This was undoubtedly the result of a cloud cover that developed late in the morning and prevailed throughout the rest of the day. By 2000 hours, one-half hour after sunset, the lake was again homothermal.

The temperature trends at 120 cm perhaps indicate that there was a net loss of heat from the bottom water to the sediments except when the entire water column was warming in the morning and again when there was circulation as the lake became homothermal in the evening.

The changing chemical conditions during the study period are shown in Figures 4 and 5. Throughout the day, conditions in a zone

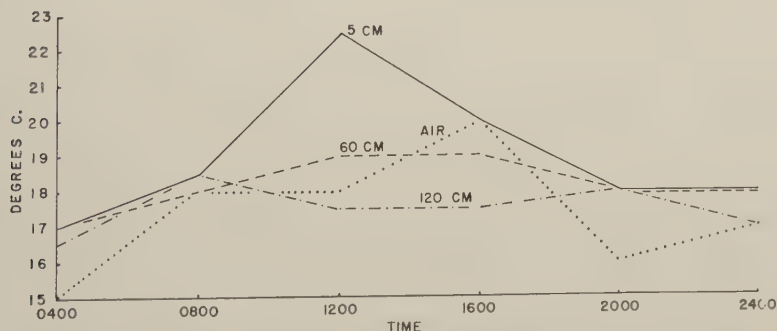


Fig. 3.—Air temperatures and water temperatures at 5 cm, 60 cm, and 120 cm in Whiskey Lake between 0400 and 2400 hours, August 2.

above 90 cm were markedly different from the conditions between 90 and 120 cm. In the surficial zone (0 to 90 cm) oxygen content varied from 5.2 to 10.2 ppm, pH varied from 9.60 to 10.40, and free carbon dioxide was as low as -37.1 ppm. Below 90 cm the oxygen content was always less than 5.2 ppm, becoming even less abundant or absent near the sediments. Also, pH was neutral or slightly acid in the bottom zone, varying between 7.91 and 6.18, and free carbon dioxide concentrations were as high as $+11.5$ ppm.

Another difference between the two zones is evident in the time-depth diagram of oxygen distribution (Fig. 5). A stable microstratification with a steep oxygen gradient persisted in the bottom zone during the entire study period, but oxygen stratification developed in

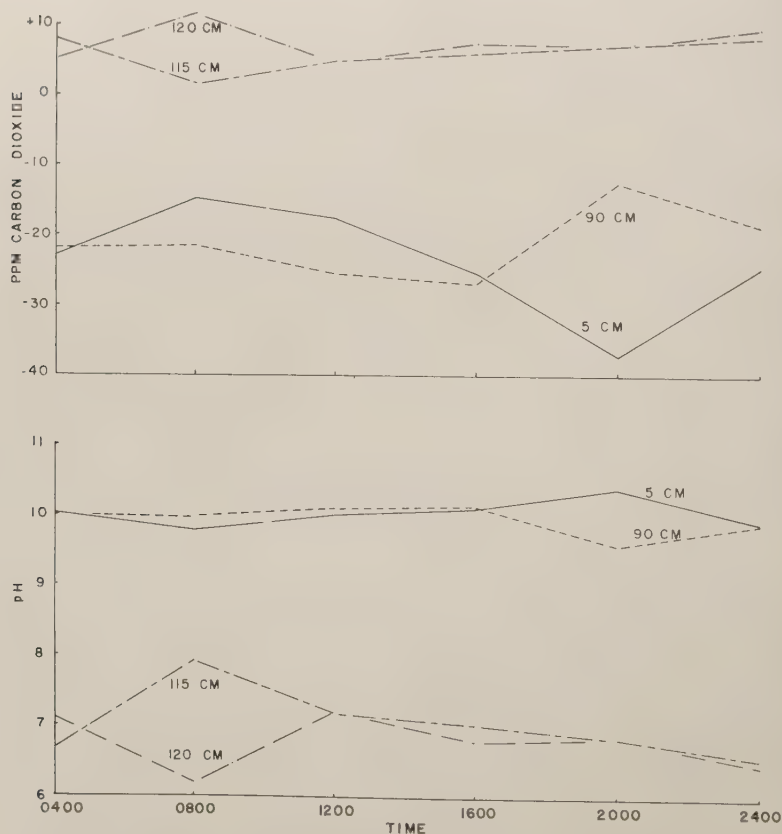


Fig. 4. The pH and apparent free carbon dioxide concentration in Whiskey Lake beginning at 0400 hours, August 2. The values at 30 and 60 cm, which virtually coincide with the values at 5 cm, have been omitted for clarity of presentation.

the surficial zone only in conjunction with thermal stratification. At 0800, when the water column was homothermal, oxygen was uniformly distributed in the surficial 90 cm, ranging between 6.16 and 6.40 ppm. The pH was also rather uniform, varying from 9.56 to 9.97. Between 0800 and 1600 hours, with the onset of thermal stratification and with increasing photosynthesis, the oxygen concentration increased to 9.13 ppm at 5 cm, to 9.83 ppm at 30 cm, but to only 6.34 ppm at 90 cm. The average oxygen increase in the surficial 90 cm was 2.10 ppm by 1600 hours. During these 8 hours the average pH increased from 9.76 to 10.02, corresponding to the removal of 12.8 ppm carbon dioxide. It should be noted that the oxygen content at 90 cm did not continue to increase after noon; it is probable that there was insufficient light for continued photosynthesis at that depth, apparently because of the overcast sky.

By 2000 hours the water column was again homothermal, and although the chemical stratification was observed to be best developed at this time, it was presumably even more distinct sometime during the previous four hours.

A study of the changes below 90 cm indicates the mechanisms of the destruction of chemical stratification in the surficial zone. Although there were large increases of pH and oxygen content during daylight in the surficial zone, the pH and oxygen concentration decreased between 90 cm and the bottom, indicating the stability of the microstratification adjacent to the sediments. But after 2000 hours, when oxygen and pH began to decrease near the surface, oxygen concentration at 90 cm increased from 5.20 to 8.81 ppm, and pH increased from 9.60 to 9.90. Evidently this was the result of the descent of warm water, rich in oxygen and with high pH, because the bottom

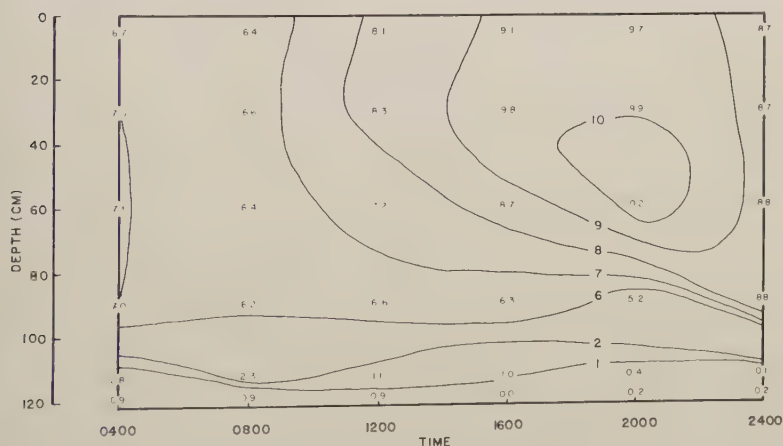


Fig. 5.—Time-depth diagram of oxygen distribution (ppm) in Whiskey Lake between 0400 and 2400 hours, August 2.

water temperature increased 0.5° between 1600 and 2000 hours. This phenomenon is reminiscent of the oxygen increase observed after dark near the bottom of Deadman Lake. The oxygen increase in both instances apparently was due to the previous cooling of the surficial water. Instability resulting from the surficial cooling enabled oxygen-rich density currents to descend, increasing the oxygen content near the bottom of the water column at the expense of the overlying water. It seems there was only a limited transport of oxygen to the bottom-most strata, because the bottom 15 cm contained at most 1 ppm oxygen at night, whereas the rest of the water column contained about 7 ppm. Evidently a persistent, complete circulation was prevented by the re-establishment of density barriers after 2000 hours when bottom temperatures decreased. Thus, oxygen transport to the bottom was not extensive most of the night; there was circulation, but only in the surficial zone of the water column, and the environmental differences between the upper and lower zones persisted during the entire diel cycle of stratification.

FURTHER STUDIES ON DEADMAN LAKE

Deadman Lake was studied again on August 12 and 13, and temperature, pH, and carbon dioxide data were gathered in addition to oxygen data. During the month since the previous visit, the depth of Deadman Lake had decreased from 70 cm to 60 cm. As a result, the stem tips of the *Myriophyllum* and *Chara* mat floated limply on the surface.

The temperature data (Fig. 6) revealed a thermal regimen similar to that of Whiskey Lake: the water column was homothermal in the morning, and stratification developed later in the day only to be disrupted in the evening. At 0800 the temperature at all depths was between 15° and 16° . After differential warming of the water column between 0800 and 1600 hours, the surface temperature was 21° , and the bottom temperature was 17.5° . This stratification was not dissi-

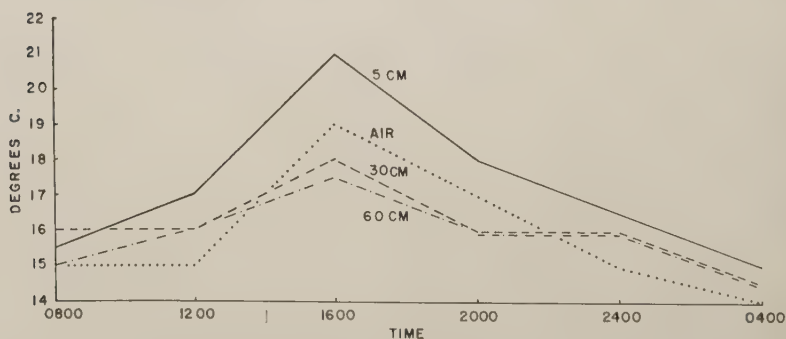


Fig. 6.—Air temperatures and water temperatures at 5, 30, and 60 cm in Deadman Lake, August 12.

pated until midnight. Even then the surface temperature was 16° and the remainder of the water column was 15.5° . After midnight the temperature of the water column continued to decrease, falling to 15° at 0400.

The oxygen, pH, and carbon dioxide data (Figs. 7 and 8) indicate a rather continuous gradient of decreasing oxygen and pH, and increasing carbon dioxide between the surface and the bottom. Although the chemical gradient was very steep between 40 and 50 cm, the upper and lower zones were less distinct than in Whiskey Lake, chiefly because there was some photosynthesis relatively close to the bottom. The gradient involved oxygen concentrations as high as 11.76 ppm at the surface to 0.0 ppm at the bottom. The pH varied between 9.61 and 10.35 at the surface and between 6.98 and 7.95 at the bottom. There was appreciable free carbon dioxide only between 50 cm and 60 cm.

As in previous studies of Deadman and Whiskey lakes there was a diel cycle of oxygen stratification associated with the development

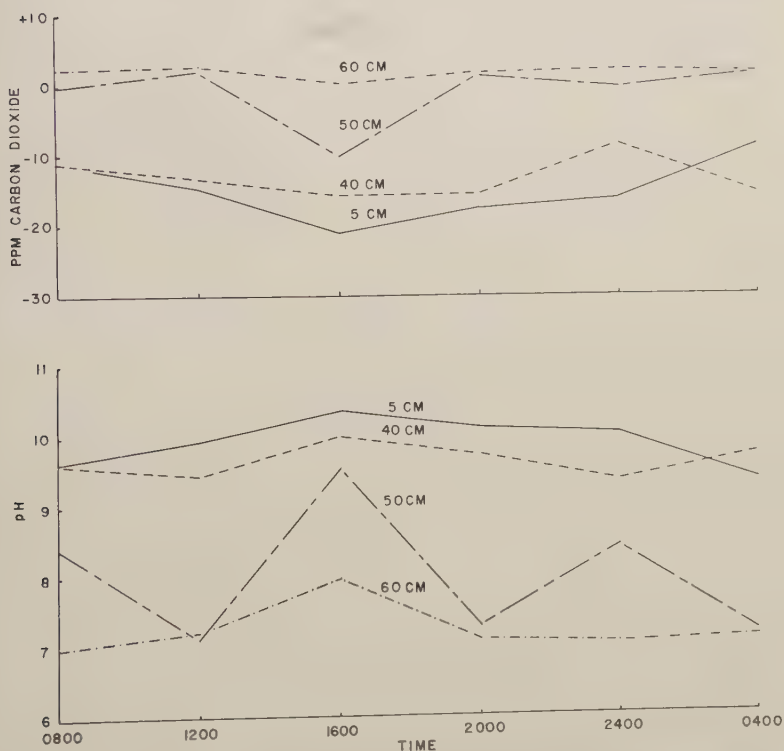


Fig. 7.—The pH and apparent free carbon dioxide concentrations in Deadman Lake between 0800 hours, August 12, and 0400 hours, August 13.

and disruption of thermal stratification. In the morning (0800 August 12, and 0400 August 13), oxygen distribution in the surficial 40 cm was uniform, averaging 5.0 ppm. But surface oxygen increased to 11.76 ppm by 1600, and the oxygen content at 40 cm increased to 7.75 ppm. This involved an average oxygen increase in the surficial 40 cm of 4.5 ppm.

The oxygen stratification deteriorated much more slowly than when it was previously observed, persisting until after midnight when the water column again became homothermal. This is not particularly surprising in view of the extraordinary denseness of the vegetation. Also, the thunderstorm on July 13 no doubt contributed to the premature disruption of the stratification that had been previously observed. Once again the disruption of stratification was associated with the peculiar nocturnal oxygen increase near the bottom of the water column, evidently another indication of the descending density currents discussed in connection with the study of Whiskey Lake.

The most obvious difference between Whiskey Lake (Fig. 5) and Deadman Lake (Fig. 8) is the oxygen increase at the bottom of the water column in Deadman Lake at 1600 hours. The lesser depth of Deadman Lake is perhaps one reason for this, but the differences of vegetation are probably also involved. Most of the plants in Deadman Lake were *Chara* and *Myriophyllum* with abundant foliage down to the bottom of the water column. In Whiskey Lake, however, the vegetation was mostly *Polygonum* with floating leaves and *Myriophyllum* with few leaves below 80 to 100 cm. Therefore, even if sunlight penetrated to the bottom of Whiskey Lake, there was reduced photosynthetic tissue.

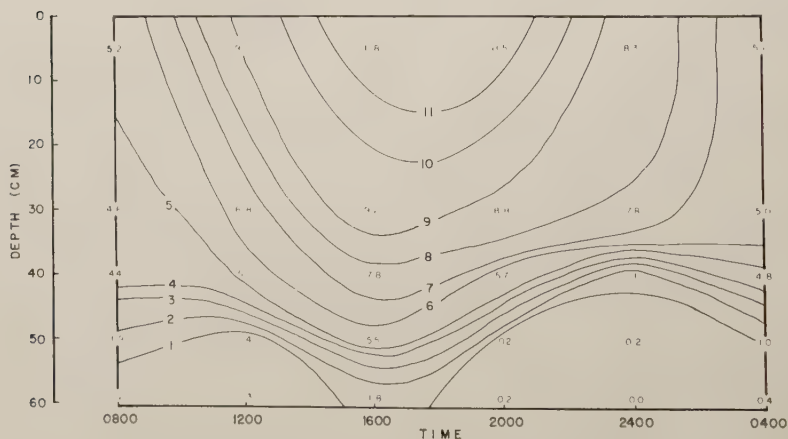


Fig. 8.—Time-depth diagram of oxygen distribution (ppm) in Deadman Lake between 0800 hours, August 12, and 0400 hours, August 13.

CALCULATIONS OF PRODUCTIVITY

All three of the studies discussed here encountered a gradient of decreasing oxygen, pH, and temperature and increasing free carbon dioxide with increasing depth among the plants. The gradient became particularly steep near the bottom of the water column so that two distinct zones were discernible. An upper trophogenic zone included in surficial 2/3 or 3/4 of the water column. Here there was as much as 10 to 13 ppm oxygen, and pH was very alkaline—as high as 10.4. Beneath the trophogenic zone there was a tropholytic zone in which oxygen concentration was typically less than 2.0 ppm. Respiration was the dominant process here, and pH was neutral or slightly acid as a consequence of carbon dioxide production. These zones preserved their identity throughout the sampling periods in the August 2 study of Whiskey Lake and the August 12 study of Deadman Lake. The zonation was also evident during the morning and evening when Deadman Lake was studied on July 13 (Fig. 1). But because vegetation was concentrated near the bottom of the water column, oxygen concentration increased considerably in the “tropholytic” zone during the afternoon. However, it is evident from the time-depth diagram that the tropholytic zone rapidly regained its identity by 2000 hours.

Buscemi (1958, Fig. 4), in his study of the environment among *Elodea*, also observed this zonation. He described an upper “photosynthetic zone” and a lower “respiratory zone.”

Superimposed upon this zonation was a diel cycle of thermal and chemical stratification that involved primarily the trophogenic zone. The elements of the cycle—uniform temperature and distribution of oxygen in the morning, development of thermal and chemical stratification during daylight, and destruction of stratification in the evening—were clearly evident in both lakes.

If the daily development of thermal density strata and the accumulation of oxygen indicate the stability of the water column, then because density stratification inhibits chemical interchange between strata, the chemical changes in the trophogenic zone can be used to estimate the rate of primary production *in situ*. Talling (1957), who studied diurnal changes in African waters, pointed out that this method has advantages because of the short time intervals involved, provided that the waters are sufficiently productive to elicit measurable changes. He also stated that there are fewer errors of defining the depth of the productive water column where photosynthetic changes are confined within thermal density strata. Attempts to estimate productivity by measuring oxygen changes in light and dark bottles have been criticized (Pratt and Berkson, 1959) and are usually considered to give low estimates (Pomeroy, 1960) because of limited water circulation and excessive bacterial respiration in the bottles. The chief shortcoming of measuring productivity *in situ* from diurnal changes, however, is that it is difficult to determine the amount of gaseous exchange between the trophogenic and tropholytic strata and

between the trophogenic stratum and the atmosphere. The loss to the atmosphere decreases with decreasing turbulence in the water column. Because of the plants, the surface of the Chuska Mountain lakes usually remained unruffled, even during high winds, so the loss of oxygen to the atmosphere is probably a relatively minor source of error. Probably more oxygen was lost from the bottom of the trophogenic zone. This was undoubtedly the case during the first study of Deadman Lake when oxygen was produced throughout the length of the water column, with no tropholytic zone to insulate the trophogenic zone from the sediments. Although it is believed that the stability of these water columns inhibited the mechanisms of oxygen loss, the following calculations of productivity must be regarded as conservative estimates.

Because the oxygen increase in the water during daylight is the total oxygen produced less any oxygen utilized in respiration, the rate of oxygen accumulation is a measure of "net" productivity. It has been mentioned that considerable interchange between the trophogenic and tropholytic zones occurred during isothermal mixing after sunset. As a consequence the oxygen content near the bottom of the water column actually increased at night. This peculiarity makes it impossible to determine the respiration rate from the available data; consequently, gross production also cannot be determined.

One of the motives for obtaining data concerning pH and carbon dioxide fluctuations was to obtain an additional measurement of productivity in terms of carbon dioxide uptake. The very high pH values complicated this attempt, however. In the first place free carbon dioxide cannot be present in waters as alkaline as these. According to Hutchinson (1957, p. 657) the carbon dioxide at pH 10.0 is present as 76 per cent bicarbonate and 24 per cent carbonate. The disturbing factor is the relative insolubility of carbonates. On August 6, determinations of methyl orange alkalinity in Whiskey Lake showed the concentration of bound carbon dioxide (carbonate) to be 32.2 ppm at the surface, 31.6 ppm at 60 cm, and 39.0 ppm at the bottom. The high carbonate value at the bottom suggests that carbonates precipitated out of the trophogenic zone and dissolved again near the bottom. Thus, carbon dioxide was removed from the trophogenic zone not only by photosynthesis but also by chemical precipitation.

The estimation of carbon dioxide by means of pH and titration curves is a method usually employed in studies of phytoplankton in open water where the pH usually varies between 7 and 9. Recently a controversy has arisen (Beyers and Odum, 1959; Verduin, Beyers, and Odum, 1960) over the relative merits of using carbon dioxide water instead of strong acid or base to prepare the titration curves. The issue apparently is irrelevant here, since all the curves they discuss are identical when the pH exceeds 8.0, regardless of the titrating agent.

However, even if the titration curves represented the empirical

relationship between pH and alkaline substances in the water, there is little doubt that the pH increases during photosynthesis represented not only carbon dioxide removal but also hydroxide production. Arens (1936) demonstrated that when aquatic plants assimilate calcium bicarbonate they release an equivalent amount of calcium hydroxide to the water. The pH-titration curve method of estimating production presupposes that a pH increase represents carbon dioxide removed by photosynthesis; but the liberation of hydroxide would also increase the pH, and the resulting estimate of carbon dioxide uptake would be too large by an amount equivalent to the hydroxide.

The quantities of carbon dioxide removed and oxygen produced in the trophogenic zone of Whiskey Lake between 0800 and 1600 hours, August 2, are shown in Table II. It is clear that if the carbon dioxide changes are used to calculate productivity, the value is more than 5 times larger than an estimate based on the amount of oxygen produced. The oxygen data are considered more reliable because they are not subject to the uncertainties associated with the carbon dioxide data.

In view of these considerations, the following calculations of net productivity are based on the accumulation of oxygen in the water column between 0800 and 1600 hours. The oxygen increase in the entire water column is utilized for the July 13 study of Deadman Lake because there was considerable oxygen production even next to the bottom. But for Whiskey Lake and the second study of Deadman Lake, the calculations are based on the oxygen increase in the trophogenic zones. Oxygen produced has been converted to carbon fixed assuming a photosynthetic quotient (O_2/CO_2) of 1.25 as recommended by Ryther (1956). The results of the calculations are shown in Figure 9.

TABLE II.—A comparison of calculations of productivity based on oxygen production and apparent carbon dioxide uptake in various strata of the trophogenic zone of Whiskey Lake on August 2

Depth	ppm O_2 increase	Chemical changes in trophogenic zone, 0800-1600 hours			Carbon fixation rate (mg C/m ³ /hr)	
		Apparent CO_2 decrease (ppm)	O_2 production rate (mg O_2 /m ³ /hr)	Apparent CO_2 uptake rate (mg CO_2 /m ³ /hr)	Calculated from O_2 data	Calculated from CO_2 data
Surface	2.78	10.65	347	1331	104	362
30 cm	3.23	22.08	404	2760	121	751
60 cm	2.22	13.24	280	1655	84	450
90 cm	0.18	5.60	22	700	6	191

In Deadman Lake 4.14 g O_2/m^2 were produced during the 8 hour period on July 13. The arithmetic mean rate of production was 517 mg $O_2/m^2/hr.$ These values represent carbon fixation amounting to 155 mg $C/m^2/hr.$ This production rate was accomplished by vigorous, growing vegetation during a very sunny day. By way of comparison, only 2.51 g oxygen were produced in 8 hours on August 12, a mean rate of 312 mg $O_2/m^2/hr.$ or 94 mg $C/m^2/hr.$ At the time of this study the *Myriophyllum* had set fruit, and the sky was often overcast. It is interesting that more oxygen was produced in the bottom 10 cm than immediately above. It is perhaps significant, then, that this was the only depth containing free carbon dioxide. Steemann Nielsen (1946) has shown that when free carbon dioxide is the carbon source, the photosynthetic rate of *Myriophyllum* is greater than when bicarbonate is the carbon source. Whiskey Lake produced 2.01 g O_2/m^2 between 0800 and 1600 hours, August 2. The mean rate was 261 mg O_2/m^2 (78 mg C/m^2) per hour.

Although the rooted plants have been emphasized in this study, chiefly because of their role in the cycle of stratification, it is not to be inferred that they are considered to be the most important from the standpoint of production. In fact, Pomeroy (1960) has shown that the marine spermatophytes, *Thalassia* and *Syringodium*, in Boca Ciega Bay, Florida, are probably no more productive than either of the other autotrophic components of the community—the benthic microflora and the phytoplankton. Where the water was 2 m deep, total community gross production was about 500 mg $O_2/m^2/hr.$ Pomeroy considers this a low value because he obtained his data by using bell jars and the light-dark bottle technique.

The average net productivity derived from the three studies in the Chuska Mountain lakes was 364 mg $O_2/m^2/hr$ (109 mg

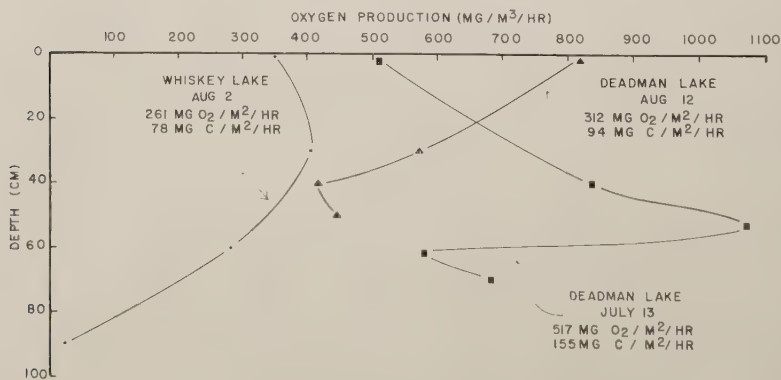


Fig. 9.—Production rates among the rooted plants of Whiskey and Deadman lakes derived from measurements of oxygen accumulation in the trophogenic zone during daylight.

C/m²/hr), approximately 1 g C/m²/day. The gross productivity would be higher than this value by an amount equivalent to the oxygen removed by the respiration of organisms in the water column and the oxygen lost to the atmosphere, the tropholytic zone, or the sediments.

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Dye Excretion as a Method for Determination of Small Mammal Home Ranges

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ABSTRACT: One hundred and twenty dyes and biological stains were tested in the laboratory for possible use in determining home ranges by excreted dyes. Dyes were mixed with beeswax, made into pellet form, and placed subcutaneously in *Mus musculus* and *Microtus ochrogaster*. Nine dyes colored the urine for four or more days (using 60-95 mg pellet) and did not depress activity as measured by activity wheels.

In field tests, dropping boards covered with filter paper were placed in a grid for recovery of colored urine from *M. ochrogaster* implanted with pellets. Home ranges calculated from the excreted dye spots corresponded closely to home ranges calculated from live trapping data for the same animals (using minimum area method).

Dyes in the same color range were found to be usable on different animals in the same area if one changed color when drops of weak acid or base solution were placed on the spots.

Most techniques designed to determine the home ranges of small mammals utilize some type of live trapping and recapture procedure. Many criticisms have been leveled against this method (Davis, 1953) but no clearly superior technique has replaced it.

The purpose of this study was first to develop a new method for determining home ranges which would eliminate some of the objectionable features of live trapping studies. The procedure developed was to implant pellets of dye into animals and determine movement by recording colored urine spots on dropping boards (Emlen *et al.*, 1957). Secondly the home ranges of some individuals were determined by conventional live trapping methods and then by the new technique to compare results obtained by these methods.

MATERIALS AND METHODS

LABORATORY

Initially 120 dyes were screened to determine their usefulness. Each dye was separately tested by preparing a pellet composed of a 1:1 ratio of dye to beeswax. Beeswax was used to form a matrix which prevented crumbling, and also slowed and prolonged absorption of dye from the pellet. Homogeneous mixing of dye and beeswax was accomplished by placing the weighed mixture of beeswax and dye granules in a paraffin oven at 56° C until the beeswax melted. This semi-liquid mixture was then removed from the oven and stirred with a glass rod until it hardened. The quantity of dye-beeswax preparation desired for a pellet was weighed in milligrams on a Roller-Smith torsion balance and then placed in a glaze-finished crucible for pulverization by a pestle.

¹ This study was partially supported by a National Science Foundation Cooperative Research Fellowship.

Preliminary experiments indicated that dye pellets placed under a rodent's skin were rapidly encapsulated by connective tissue, and within 2-4 days absorption and excretion of the dye largely ceased. It was found that when 8 mg of cortisone acetate powder were added to 50 mg of dye-wax preparation, encapsulation was retarded until about 14 days after pellet implantation. The thoroughly mixed dye-beeswax-cortisone preparation was made into a compact cylindrical pellet by tamping the mixture into a hole in a brass block. The diameter of the dye pellets thus formed was 2.38 mm (3/32 inch). Each pellet was brought to the desired weight or length by cutting portions off the end with a scalpel.

Laboratory white mice (*Mus musculus*) were used for the preliminary screening of the dyes. The pellets used in laboratory mice weighed from 35-40 mg. Each pellet was inserted subcutaneously into lightly anesthetized mice through a small incision in the dorsal skin about one inch anterior to the base of the tail. Then it was moved forward beneath the skin with a stroking action of the fingers to an infrascapular position. A single, small surgical clamp or a drop of celloidin was sufficient to close the incision.

Mice containing dye pellets were placed in wire-bottomed cages with food and water available at all times. A large piece of white filter paper was placed under each cage so that the urine could be checked for dye coloration. The criteria set for the screening tests were that the dye should color the animal's urine for several days (arbitrarily about seven), and that the dye should not produce any apparent adverse effect on the animal. If a dye did not meet these conditions it was discarded without further testing. Filter papers were changed at 24-hour intervals after pellet implantation until the urine spots no longer displayed any dye coloration.

Dyes that gave promising results were tested on specimens of *Microtus ochrogaster*. This second screening procedure was the same as that used in the laboratory mice. The pellet weights used in adult *Microtus* were from 65-90 mg.

Tests in activity wheels were conducted to determine the effect of dye pellets on a vole's activity. The number of revolutions for each 24-hour period was recorded throughout the activity experiments. After the normal activity of each specimen was obtained for a period of seven days, a pellet was implanted, and the individual's activity observed for another seven day period. Animals were weighed before being placed in the activity wheels, at the time of pellet implantation, and after the experiment was concluded, to give another index of the animal's health. Only male *Microtus ochrogaster* were used, to avoid variations in activity due to the estrous cycle. All dyes selected for use in the field were tested on at least three animals in the activity wheel experiment.

Two types of experiments were used to determine the effect of the pellet implantation procedure on activity. A mock pellet implantation was performed on five animals. This consisted of making the small

opening in the skin, probing forward with forceps, and then closing the opening with a surgical clamp without placing any dye pellet subcutaneously. The second type of control was similar to the first except that inert beeswax pellets (the same size as the dye pellets) were placed under the skin of five prairie voles. These experiments were designed to determine the effect of the implantation operation on activity and the effect of the physical presence of a subcutaneous pellet on activity. The procedure for determining activity was the same for all the experimental animals.

FIELD

Missouri River Island

During a ten day period in December, 1959, a comparison was made of home range estimates obtained by live trapping methods and by the use of excreted dyes and dropping boards. The study was made on an island in the Missouri River, 18 miles southwest of Columbia, Missouri. Live traps of the type described by Blair (1941) were used. The trapping grid was composed of ten rows of ten traps each, spaced at 30 foot intervals. The grid covered an area of 2.06 acres. The plot was checked twice daily for five days; a total of 1,000 trap nights. Hamilton's (1937) scheme of toe clipping was used to mark the animals before release, after the initial capture.

An area covering about one-third of the trapping plot was found to have a rather high microtine population so the excreted dye home range study was conducted there. Dropping boards were placed at or near each former trap site, in a vole runway whenever possible. Boards were also placed at the halfway points of the 30 foot intervals in the trap grid, making the dropping board interval 15 feet. One hundred boards were used in the chosen portion of the trap quadrat. The dropping boards were made of $\frac{1}{8}$ inch of $\frac{1}{4}$ inch thick masonite and were 4 inches square. White filter paper was affixed to the dropping boards with small pieces of cellophane tape at the corners. The white surface made possible the identification of colored urine spots. Initially some white-painted dropping boards were also included.

Specimens of *Microtus ochrogaster* which had been previously trapped in the recapture home range study were implanted with dye pellets on the sixth day of trapping. Five such animals were marked in the field using the same diameter and weight of pellet as in the laboratory. Each vole was released at its point of capture after recovery from anesthesia.

In some cases, two dyes resulted in urine of the same color. These dyes were still usable in the field if the urine spot from one or both changed color when a drop of acid or base solution was placed on it. For example, one vole was marked with safranin and another with superchrome violet; both color the urine red. The latter dye turns violet when a drop of 10 per cent potassium hydroxide is placed on a dyed urine spot, but the former stays red. Bottles of 10 per cent KOH and 10 per cent HCl were used in this dye pellet home range

test to conclusively identify urine spots which could have been from either one of two animals.

All live traps were closed after pellets were placed in voles, to prevent any limitation of the animals' normal movements due to recapture. Dropping boards were checked once each day over the five days following pellet implantation, for vole droppings and urine spots. Rodent droppings were noted and removed from the dropping boards at each visit to the grid. Boards with urine spots were replaced with clean ones. When the filter paper covers on dropping boards became dirty or stained from vegetation, they were replaced with clean boards.

Home range was calculated by the minimum area method from both sets of data. This method appeared to be the most valid, considering different grid intervals were used.

University of Missouri Entomology Farm

A second test comparing standard live trapping to the use of excreted dyes for home range determination of *Microtus ochrogaster* was made in a field on the University of Missouri Entomology Farm, $\frac{1}{4}$ mile southwest of Columbia, Missouri. A grid of 56 traps was placed at 25 foot intervals in a neglected pasture. The study took place over a 14 day period in late March and early April, 1960.

The same general methods used in the Missouri River island study were repeated in this test. The trapping grid was composed of seven rows of eight traps each and covered an area of about one acre. The traps were baited with pieces of apple because this bait was found to be quite useful in the spring for enticing microtines into traps. Peanut butter is of little value as a bait when new green vegetation is present. The plot was checked twice daily for seven days, a total of 1,400 trap nights. Traps were set in the most favorable location nearest each marked trap station in the grid.

An area covering about one-half of the trapping plot was found to have an adequate microtine population for excreted dye home range study. A dropping board interval of 12.5 feet was used, *i.e.*, boards were placed at trapping stations and also at halfway points. A total of 116 dropping boards were used in the chosen portion of the trap quadrat. White filter paper was affixed to all boards.

Specimens of *Microtus* which had previously been trapped at least four times were implanted with dye pellets after the seventh day of trapping. Six animals were marked in the field with pellets weighing 64-69 mg. Live traps were closed and the dropping boards were checked once each day for seven days. Vole droppings were removed and filter papers were replaced when necessary throughout the study period. Home range was calculated by the minimum area method for both live trapping and excreted dye data.

RESULTS

LABORATORY

The results from initial screening of 120 dyes and biological stains

for potential use in home range determination studies, eliminated many dyes from further consideration (Brown, 1960). Several dyes were eliminated because they killed the animal within a few days after implantation. Others colored the urine for a desirable period of time, but were rejected because the mice were obviously ill. Several dyes which colored the urine only 3-4 days were retested by increasing the amount of dye per pellet to two parts dye to one part beeswax. Doubling the concentration of dye per pellet had little effect in extending the period of urine coloration. Occasionally this increased dye concentration caused the animal to appear ill when the 1 dye: 1 beeswax weight pellet did not.

Eighteen dyes which showed promise in *M. musculus* were tested using *M. ochrogaster* in activity wheels (Brown, 1960). Most animals demonstrated considerable variation from day to day in the number of revolutions performed in the activity wheels. Depression of an individual due to a dye pellet was expressed by a marked reduction in wheel revolutions following implantation. The body weights of all animals in the activity wheels tended to decrease a few grams during the first seven days. This was probably because the animals expended more energy than they did in the holding cages. Most animals recovered a portion of this weight loss during the second week in the activity wheels regardless of the dye used or experimental manipulation.

Table I lists the nine dyes considered usable in home range determination and their color reactions. None of these dyes produced activity depression or other observable adverse effects under the test conditions. Acridine red and fluorescein are suggested as second choices because their colors are not as long-lasting as those of safranin-O and tropaolin-O respectively. Fluorescein can be separated from other orange-yellow dyes on the basis of fluorescence, but the field use of this was questionable.

TABLE I.—Dyes suitable for use in urine coloring experiments

Dye	Substitute dye	Excreted color	Color at acid pH	Color at basic pH
Safranin O	Acridine Red	Red-pink	Same	Same
Superchrome violet B		Red-pink	Same	Violet
Tropaolin O	Fluorescein	Orange-yellow	Same	Same
Meta cresol purple		Orange-yellow	Red-pink	Purple
Phenol red		Orange-yellow	Same	Red-pink
Methyl orange		Orange-yellow	Red-pink	Same
Fast green FCF		Green-blue	Same	Purple

Attempts were made to use fluorescein with other dyes; for example, to produce a fluorescent-safranin colored urine. Pellets were made from a 1 fluorescein: 1 dye: 1 beeswax mixture (by weight). Both colors were found to separate out when the urine colored by this type of pellet was placed on white filter paper. Fluorescein's color dominated the urine for the first 2-3 days after implantation; this then largely faded, and the other dye dominated the urine color the rest of the test period. Combining fluorescein with other dyes was therefore discarded because of variability in the urine color produced and the inconclusiveness of the fluorescence of colored urine spots.

The dyes listed in Table I fall into only three color groups, but dyes within each group are identified from one another by their colors in the acidic or basic pH range. Therefore seven different animals could be marked in the same area, and the dye in their urine spots identified with drops of acid and base solutions.

The sham implantations and the inert beeswax pellet implantations caused no depression of activity in *Microtus*. The simple implantation operation and the physical presence of a pellet under an animal's skin were thus eliminated as factors that prevent normal activity.

FIELD

Missouri River Island

A comparison of the number of records per animal using the excreted dye method and the live trapping method in a five day period is presented in Table II. The total number of colored urine spot records was slightly higher than the total number of trapping records for the five *Microtus*, but not significantly so. Table II also presents the minimum home range calculated in square feet from both sets of data, where such calculations could be made. The revealed home ranges using the excreted dye method were larger than the live trapping home range figures in the two cases calculated. Since the study period was only five days for each method, not enough

TABLE II.—Comparison of live trap and excreted dye home range determination for individual *Microtus ochrogaster*

Toe clip number	Sex	Dye	Number of trap records	Number of urine records	Live trap home range in sq. ft.	Excreted dye home range in sq. ft.
15	M	Safranin O	4	6	450	787.5
18	M	Meta Cresol	3*	1		
		Purple				
35	M	Superchrome	3	5	450	900
		Violet B				
44	F	Fluorescein	2**	4		675
45	M	Phenol Red	1	0		

* Captured in same trap.

** No home range calculation possible using minimum area method.

records for a more precise calculation of home range were obtained.

From 6 to 20 per cent of the dropping boards had droppings and/or urine spots on them each day the plot was checked. The lowest figure was noted following rainfall of .77 inches. The trapping success ranged from 27 to 36 per cent daily during the live trapping study on the part of the quadrat used for the excreted dye test.

Painted dropping boards were found to be inferior to filter paper covered ones, because when the urine evaporated, identification of the dye was nearly impossible on painted boards. Evaporation of urine on filter paper did not cause the dye color to fade or change. Rain washed the filter paper free of fluorescein spots, but did not affect safranin O, superchrome violet, or meta cresol purple. On the fourth day of the excreted dye test, 0.4 inch of snow fell, most of which melted upon contact with the moist vegetation. This light snowfall apparently did little to deter deposition of urine and droppings on the boards.

The filter paper on the dropping boards withstood weathering well during the five days. The paper did not become torn or detached from the boards even when wet. The paper on some boards had to be replaced during the period of rain and light snow when it was stained with brown drippings from dead vegetation.

University of Missouri Entomology Farm

Excreted dye home range determination is compared to live trapping home range determination in Table III. The number of trapping records were nearly twice as great as the total number of colored urine spot records for the six *Microtus ochrogaster*. Insufficient records were obtained from all but two animals to permit comparisons of the two methods. However, in all cases the sites recorded by the two methods were within short distance of each other.

Home range configurations using both methods tended to con-

TABLE III.—Comparison of live trap and excreted dye home range determination for *Microtus ochrogaster*

Toe clip number	Sex	Dye	Number of trap records	Number of urine records	Live trap home range in sq. ft.	Excreted dye home range in sq. ft.
12	M	Fast Green	10	8	937.5	937.5
13	M	Safranin O	7	7	312.5	468.8
14	F	Phenol Red	6	1	312.5	
16	M	Superchrome Violet B	7	3	2187.5	234.4
22	M	Meta Cresol Purple	4	3*	312.5	
23	F	Fluorescein	4	0	625.0	

* Two records were at same station.

form rather closely in cases where sufficient records were realized. As Figure 1 demonstrates, excreted dye home range determination substantiates the validity of live trapping home range determination in voles. The home ranges of animals No. 12 and 13 show similar boundaries (with minor variations explained on the basis of difference in grid size) using both methods of determination.

From 2 to 8 per cent of the dropping boards had droppings and/or urine spots on them each day the plot was checked. There was no significant precipitation during the test period. The trapping success ranged from 5 to 30 per cent daily during the live trapping study of the part of the quadrature used for the excreted dye test.

DISCUSSION

Probably the most important factor determining the optimum weight and length of dye pellet to be used in an animal, is the total surface area of the pellet available for dye absorption. In general, a

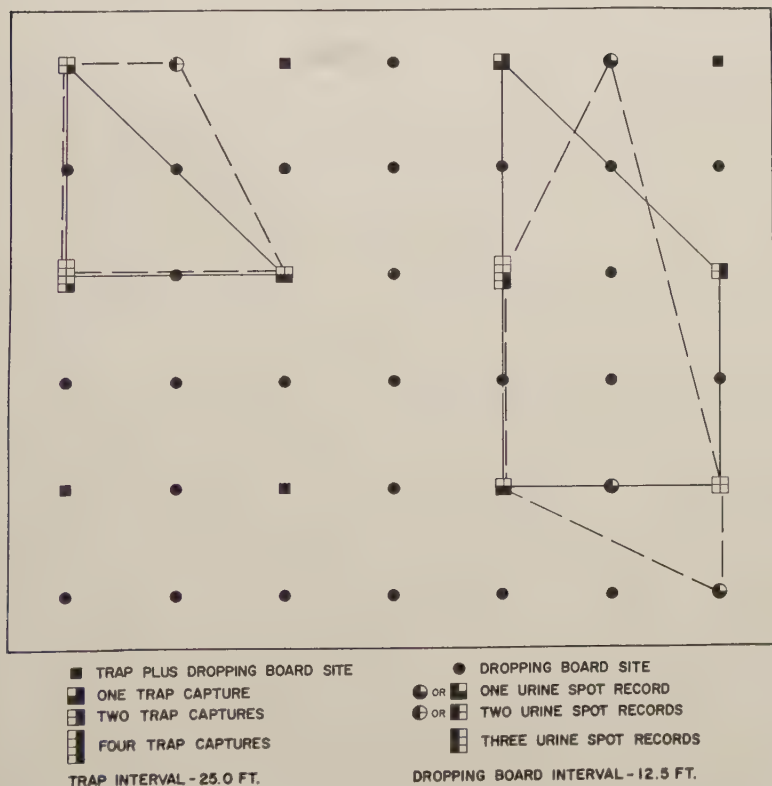


Fig. 1.—Comparison of the home ranges of two male *Microtus ochrogaster* when determined by the excreted dye and live trapping method.

pellet of twice the surface area of those recommended for use in *Microtus ochrogaster* was found to depress activity, and a pellet of half the surface area proved too small to color the urine long enough to be useful.

Further experiments with the group of dyes which were discarded because they failed to color the urine long enough, might extend the urine coloring period in some cases. Possible variations are (1) the use of different inert bases for the pellets, (2) increasing the concentration of dye per pellet, and (3) the use of pellets with a larger absorption surface.

None of the brown or black dyes screened was found to be satisfactory; testing more dyes of these colors might produce additional means of marking more animals. No really adequate blue-green dyes were realized from the screening experiments. Most of them colored the urine strongly, but depressed activity. Fast green was elected for final use because it did not depress activity, unfortunately it colors the urine only about four days. There is a possibility that further experiments with the blue-green range of dyes will provide a longer lasting substitute for fast green.

Incorporation of a radioactive isotope such as P32 into dye pellets would double the number of animals that could be marked in a given study area. For example, one animal could be implanted with a non-radioactive safranin O pellet and another with a radioactive safranin O pellet. A Geiger-Muller counter could then be used as Miller (1957) did, to distinguish the excretions of two such animals.

A method whereby fluorescein could successfully be used in combination with other dyes, and the excretion identified could probably be developed using simple photofluorometric methods. Photometric methods could also be used to identify two dyes that appear to be the same color and cannot be identified by the simple pH, color change method. Thus with refined techniques an impressive number of individual dyes, dye combinations, and dye-radioactive isotope combinations could be used to mark a large number of mammals on a study plot.

A number of advantages can be listed for the excreted dye method of home range determination over other methods. (1) Repeated handling of the animals is not necessary; they need to be live trapped only once. (2) In live trapping methods for home range determination, each animal spends a greater or lesser portion of its time confined in a trap, when it would normally be moving about its home range. This period of exposure and limitation of activity is avoided when the excreted dye home range method is applied. (3) Animals are not attracted to dropping boards by food as they are to baited live traps or the dye feeding stations of New (1958). (4) A large number of boards can be placed in a small interval grid (such that dropping boards occur every 5-15 feet) without disrupting the normal movements of small mammals. A grid of live traps placed at intervals approaching these distances would severely hamper the animals' move-

ments to the outer extent of their home ranges; each animal would probably be caught repeatedly in one or two traps. (5) The ability to use a small grid interval without disrupting movement, enhances the calculation of an accurate and meaningful home range. If a boundary strip is added to the minimum home range, it would be small and less likely to produce an erroneous home range figure than a larger one would. (6) Dropping boards need be checked only once a day under normal conditions, thus the animals are not continually disturbed by the observer as was the case in Godfrey's (1954) method utilizing radioactive leg bands and Kaye's (1960) method using gold-198 wires. (7) To some extent, each animal's range of movement in a 24-hour activity period is revealed.

A criticism of using excreted dyes is that the urine coloration does not last indefinitely. Also, it is possible, though not indicated in the field test, that male and female rodents are not equally inclined to use dropping boards. Although activity wheel results do not indicate it, a third criticism might be that the mechanical irritation of a pellet could cause increased activity or abandonment of the home range.

Since shrews and several small rodents in addition to *Microtus ochrogaster*, are known to utilize dropping boards (Emlen *et al.*, 1957), the home ranges of these mammals can be determined by the excreted dye method. In regard to the use of excreted dyes to mark animals when snow is present, it is possible that the method could be used on certain carnivores or even ungulates such as deer, once the proper pellet size is determined. Finally this technique might prove useful as a method for estimating population size in a modified Lincoln Index study (Lincoln, 1930).

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Patterns of Distribution of Sugar Maple, *Acer saccharum* Marsh., in Northern Cape Breton Island¹

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ABSTRACT: An investigation has been made of the distribution patterns of *Acer saccharum* Marsh. on, and in close proximity to the limit of the range of the species in, northern Cape Breton Island. The limit of the range of the species cannot now be clearly delineated at sea level, but at greater elevations varies from altitudes of the order of 800 feet on seaward slopes to 1300 feet inland. In both primeval and second growth areas the density and dominance of the species vary widely, with a trend toward lower stocking with increasing altitudes. In some areas the limit of the range is marked by widely scattered trees whereas in others the density of the species is fairly high. Irrespective of stocking, there is no gradual transition in size toward a depauperate form or a marked decrease in vigour upon approaching the limit of the range of the species. On the basis of present evidence it is difficult to decide whether the limit of the range is stationary, advancing or retreating.

INTRODUCTION

Studies in the water economy of forest trees have been conducted in Nova Scotia for the past several years. In this program some attention has been given to species distribution patterns, and to patterns of morphological and physiological variation within species, with particular reference to sugar maple, *Acer saccharum* Marsh. This species constitutes extremely favorable material for investigations of this nature. In northern Cape Breton Island, the focal point of this work, sugar maple occurs over a very wide spectrum of sites, bounded on the one hand by rich bottomlands and on the other by a geographically well-defined complex of stations which marks the apparent limit of its range. Observations on the occurrence of sugar maple, with particular reference to conditions on the limit of the range of the species in northern Cape Breton, are presented in the following paragraphs. An empirical approach to the problem has been adopted, and in discussing the results speculation regarding causal relations has been avoided.

PHYSIOGRAPHY, SOILS, AND CLIMATE

The physiography of Cape Breton Island has been treated at length by Goldthwait (1924). Likewise Nichols (1918) has described in detail the topography of the northern reaches of the area. Similarly, Roland (1944) has included a brief but useful physiographic survey of the region in his flora. Consequently a very short review of the

¹ Contribution No. 688, Forest Biology Division, Research Branch, Canada Agriculture, Ottawa, Canada.

main features of the experimental area will serve the needs of the present discussion.

The bulk of northern Cape Breton Island comprises a massive plateau composed largely of Pre-Cambrian granites, syenites, quartzites, and slates. Goldthwait (1924) tentatively concludes that peneplanation of this upland surface was completed in the Cretaceous period, and that subsequently the entire region suffered a gentle upwarping. Several cycles of uplift and erosion and one or more glaciations are thought to have fashioned the contemporary morphology of the region.

From seaward the surface of the tableland is strikingly flat, although in actual fact the elevation ranges from 1200 to approximately 1800 feet above sea level. In some areas the plateau extends to the sea whereas in others a narrow coastal plain intervenes. The tableland is being dissected by a number of short, very swift rivers and streams, and in consequence is normally flanked, both on the coast and along the river valleys, by steep, tree-covered slopes. To the southwest and along the southern edge of the escarpment the approaches to the plateau remain steep, but the average elevation of the tableland is somewhat less.

In addition to the central mass of the plateau, there are several outlying regions of considerable area characterized by the same rock structure and type of surface, but with a somewhat lower average elevation. These outliers, together with the main body of the tableland, have probably been glaciated. However, our knowledge of the geography of the Pleistocene in northern Cape Breton Island is not extensive (Livingstone and Livingstone, 1958).

Slightly more than half of Cape Breton Island is occupied by lakes and lowlands. The latter are coincident with areas of soft sedimentary rocks of Carboniferous age (Goldthwait, 1924). Rolling hills of subdued outline seldom exceeding 500 feet in height are characteristic of the lowland regions.

Until recently there had been no extensive mapping of the soils of northern Cape Breton Island. However, the Experimental Farms Service of the Canada Department of Agriculture has recently completed a soils survey of the region, and the results are expected to appear in the near future. Several years ago the author made an examination of approximately 30 soil profiles located in hardwood areas in the northern reaches of the Island, and found a display of soil depths ranging from 12 inches on steep slopes to 4 feet in moist bottomlands. The soils of practically all sites examined were classified as sandy loams with an infrequent silt loam or loam.

Although meteorological observations are made at several locations in Cape Breton Island virtually no data are available regarding conditions encountered on the plateau. Useful summaries of data gained at coastal and inland observing stations may be found in publications of the Meteorological Division, Canada Dept. of Transport (1948), in Baughner and Thomas (1948) and Thomas (1953).

RANGE OF SUGAR MAPLE

There is considerable evidence to suggest that the northernmost reaches of Cape Breton Island are approximately coincident with the northern limit of the range of sugar maple. In recent years, despite considerable searching, Fernald (1911) was unable to collect the species in Newfoundland, the southern coast of which lies 30 sea miles north of Cape Breton Island. Likewise, in the eighth edition of Gray's Manual (Fernald, 1950), Newfoundland is not included within the range of sugar maple. Similarly, Rouleau (1956) does not include the species in his recent check list of the vascular plants of this province. The curators of the herbaria of the National Museum of Canada, the U.S. National Museum, and the New York Botanic Gardens, in answer to the author's inquiry, have replied that no specimens of *Acer saccharum* from Newfoundland are to be found in their respective collections. Other workers, including Hutchinson (1918) and Nichols (1918), indicate that this species does not extend into Newfoundland.

Perry (1931) and Erskine (1945) do not include *Acer saccharum* in the flora of St. Paul Island. It is noteworthy that the latter land mass is disposed only 10 sea miles to the northward of northernmost Cape Breton Island.

However, a contrary view with respect to the occurrence of sugar maple in Newfoundland has been expressed by several workers, including Bell (1897), Gleason (1952), Godman (1957), Harshberger (1911), and Little (1953). Likewise, Nichols (1935) appears to have reversed his opinion in a paper subsequent to that cited above.

METHODS AND RESULTS

Attempts by the author to delineate the northern limit of the range of sugar maple at sea level and at minor elevations in northernmost Cape Breton have been inconclusive. On the west coast of the Island, walking trips have been made as far north as Pollett Cove (Fig. 1) and the species observed consistently en route. On the east coast the species is common along the road between Capstick and Meat Cove. In the area of Cape St. Lawrence Light sugar maple has been found approximately one-half mile south of the coast at an elevation of the order of 320 feet. To the north of this station the area has been burned several times and individuals of the species have not been observed in the young birch-poplar-cherry association which is now found on the site. Similarly, in the area of Cape North—Money Point Light sugar maple has been found frequently along the trail to the lighthouse, the northernmost sighting being approximately one-half mile south of the Light at an elevation of 125-175 feet.

Elsewhere, however, the limit of the range of the species as affected jointly by latitude and altitude has been established fairly readily. To trace the distribution of the species the following procedure was adopted.

At or near the foot of each of a number of pre-selected routes to the plateau, a control point was established and its elevation determined. On three occasions advantage was taken of stations of known elevation established by the Geodetic Survey of Canada. In the course of the ensuing ascent, wet and dry bulb thermometer and atmospheric pressure readings were made at intervals of 10 minutes at the bench mark. Following stabilization and comparison of instruments at the datum, a climbing party equipped with two aneroid barometers and a sling psychrometer moved upwards from the datum along a predetermined mean line of advance recording temperature and pressure at 10 minute intervals synchronously with readings being taken at the datum. However, at higher elevations, upon approach-

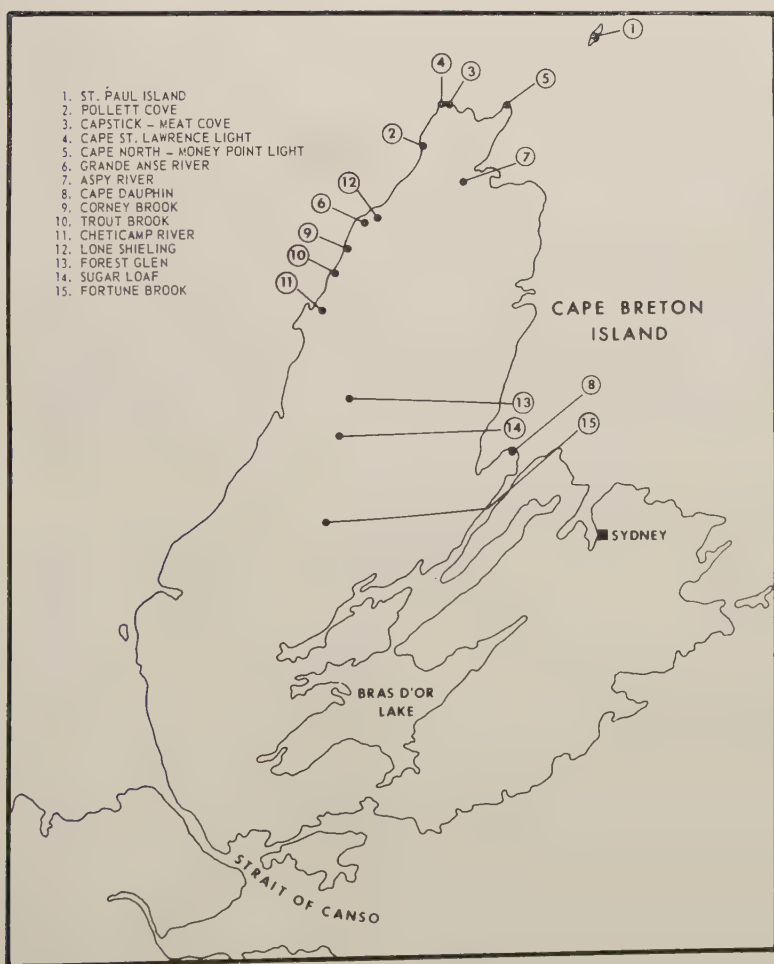


Fig. 1.—Map of Cape Breton Island.

ing the altitudinal limit of the range of sugar maple, the progress of the party was directed from sample tree to sample tree with readings taken as requisite without reference to a time interval. Upon establishing the apparent altitudinal limit of the species, temperature and pressure measurements were made at several trees, and the climbing party next continued forward a distance of 10 to 20 chains with readings being taken at frequent intervals. An offset of varying length at right angles to the mean line of advance was then made, and the climbing party next moved down into the range of the species along a reciprocal course. Upon regaining contact with individual sugar maple trees the apparent limit of the range was again delineated, time, temperature, and pressure measurements being made at a number of trees.

As noted above, at the commencement of each climb, barometers were left to become stabilized at the datum point and then read. Wet and dry bulb temperatures were recorded simultaneously. Pressure and temperature trends were subsequently followed closely at the datum during the ascent. At the conclusion of the operation, all instruments were read again at the bench mark following stabilization. With sufficient justification, as judged by the observed barometric tendency at the datum during the course of the climb, a straight line or otherwise was drawn connecting the initial and final datum readings of the instruments accompanying the climbing party. Intermediate control values, in time, were taken from the resulting graphs. To minimize the possibility of interpretative errors in pressure readings, ascents were made only under favorable weather conditions. A further means of control was achieved through the plotting of surface analysis charts which yielded information regarding the synoptic picture. Elevations were determined with the aid of the following formula (Brunt, 1952).

TABLE I.—Elevation of limit of range of sugar maple at various locations in Cape Breton Island

Position	Transect	Location	Exposure	Elevation at limit (ft.)
Cape Dauphin	A	Coastal	SE	810
Corney Brook	B	Coastal	W	720
Trout Brook	C	Coastal	NE	785
Cheticamp River	D	Slightly inland	N	782
Aspy River	E	Slightly inland	SE	1355
Lone Shieling	F	Slightly inland	NE	1120
Forest Glen	G	Inland	E	1359
Sugar Loaf	H	Inland	SE	1338
Fortune Brook	I	Inland	SW	1247

$Z = 221 T (\log p_0 - \log p)$ where

Z = height of station in feet above datum

T = average of temperature readings at bench mark
and at observing station in degrees Absolute

p_0 = pressure in millibars at datum at time t

p = pressure in millibars at observing station at time t

Results gained in a number of climbs to the plateau are included in Table I.

Distributional patterns in sugar maple were traced by means of transects extending from bottomlands to the upper reaches of the plateau and oriented as requisite. Along these transects all trees 3 inches and above in diameter, and located within one-quarter chain of the center line were tallied.

Stand and stocking relations were investigated through the medium of 0.2 acre plots established in a wide variety of sites. Within plots all trees 3 inches and above in diameter at breast height were tallied by species, crown class, and condition, and by azimuth and distance from a central point, the center of the plot. Sample trees were felled at the plots, and later used for purposes of analysis and for morphological and histological examination.

TABLE II.—Structure of lowland, second growth, hardwood stands in northern Cape Breton Island

D.B.H.	Plot No. 1		Plot No. 2		Plot No. 3	
	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species
3	4	7	--	--	--	1
4	14	18	4	6	6	11
5	6	6	7	6	7	11
6	10	10	6	6	10	12
7	7	7	12	17	9	10
8	5	5	7	8	4	4
9	1	1	12	15	6	7
10	4	5	7	11	7	7
11	4	5	7	9	11	11
12	1	1	--	--	5	5
13	3	3	1	3	1	1
14	--	--	--	3	3	3
15	1	2			1	1
16	3	4			1	1
17	--	--			1	1
18	--	--				
19	--	--				
20	--	1				
Age (yrs.)	65	--	90		110	
No. of trees per acre	315	375	310	425	360	420
Basal area per acre (sq. ft.)	115	144	113	172	166	173

DISTRIBUTIONAL PATTERNS — LOWER, MIDDLE,
AND UPPER SLOPE STANDS

The percentage of sugar maple in second growth bottomland stands in northern Cape Breton Island ranges from low to very high, with almost pure stands of the species frequently being encountered. Density is high and growth in height is frequently good. The structure of several such stands is outlined in Table II.

In second growth areas, in passing upward toward the surface of the plateau, some variation in form and considerable fluctuation in the density and dominance of sugar maple are encountered. Frequently, therefore, the distinctly sugar maple characteristic of the forest, so clearly evident in bottomland sites, is lost.

Stand and stocking relations in old growth bottomland stands may be investigated at a few localities in northern Cape Breton Island. In these stands density apparently is normal, and the percentage of sugar maple varies widely. Basal area in better stands reaches 230 sq. ft. per acre, with sugar maple occasionally constituting 95 per cent of this figure.

TABLE III.—Percentage composition in transects in second growth and
primeval forests in northern Cape Breton Island
Transect No. 1 (second growth)

Dist. from datum (chains)	No. of trees/acre		Basal area/acre (sq. ft.)	
	Sugar maple	All species	Sugar maple	All species
1	60	400	9	87
3	--	140	--	85
5	--	180	--	61
7	--	220	--	104
9	20	260	2	54
11	20	260	4	72
13	120	300	29	65
15	100	180	34	69
17	160	260	100	103
19	220	300	118	162
21	60	140	11	74
23	40	200	45	79
25	120	200	88	99
27	180	300	94	146
29	120	240	59	102
31	60	340	29	126
33	--	180	--	81
35	--	300	--	57
37				
39				
41				
43				
45				
47				
49				

Transect No. 2 (second growth)

Dist. from datum (chains)	No. of trees/acre		Basal area/acre (sq. ft.)	
	Sugar maple	All species	Sugar maple	All species
1	180	380	83	147
3	140	340	28	106
5	80	260	14	61
7	110	120	25	29
9	200	260	43	67
11	--	420	--	117
13	60	220	6	46
15	160	300	43	72
17	80	280	18	87
19	120	360	21	50
21	80	240	48	101
23	60	220	37	132
25	60	200	43	89
27	120	140	57	61
29	20	40	16	20
31	140	140	103	103
33	40	40	9	9
35	--	80	--	85
37	--	140	--	93
39	--	120	--	64
41	--	120	--	56
43	--	20	--	3
45	--	160	--	90
47	--	200	--	93

Transect No. 3 (Primeval)

Dist. from datum (chains)*	No. of trees/acre		Basal area/acre (sq. ft.)	
	Sugar maple	All species	Sugar maple	All species
1	80	120	28	84
3	120	180	45	107
5	140	180	97	111
7	180	180	186	186
9	160	160	144	144
11	80	80	128	128
13	160	240	27	108
15	100	200	44	142
17	60	120	40	52
19	160	200	49	103
21	160	180	112	148
23	80	180	43	106
25	60	240	32	136
27	20	180	5	72
29	--	220	--	62
31	--	500	--	95
33	--	120	--	73
35	--	40	--	14
37	--	180	--	37
39	--	20	--	9

* No trees 3 inches or more in diameter were encountered at 41 to 49 chains from datum.

Despite the proximity of the examination area to the apparent northern limit of the range of sugar maple, individuals exceeding 100 feet in height and 30 to 35 inches in DBH, though not common, occur in the valley of the Grande Anse River. In second growth stands of good quality co-dominant trees frequently reach heights of 60 feet in 50 years.

Passing upward toward the surface of the plateau in old growth, undisturbed areas, the density and dominance (basal area) of sugar maple vary considerably, but the distinctly sugar maple characteristic of primeval bottomland stands is sometimes retained, particularly at lower and middle elevations. Data gained in transects from bottomland sites to the limit of the range of the species in second growth and primeval stands are summarized in Table III.

Irrespective of conditions obtaining in nearby bottomlands, many hardwood areas on the upper flanks of the plateau have not been logged. However, the history of these stands may differ widely, and the age class distribution pattern is complicated. Despite the age of many of these trees (200 years), the height of the average co-dominant is not great, seldom exceeding 45 feet, with a diameter at breast height of less than 14 inches. In these upper level stands the percentage of sugar maple is frequently high and the density of stocking is usually normal (Table IV).

Sugar maple trees in stands in southern and central Cape Breton Island located on the surface of the plateau but growing at elevations below the altitudinal limit of the species are commonly short and of poor form, and the density of the species is commonly low.

DISTRIBUTIONAL PATTERNS — RANGE LIMIT STANDS

Topographic conditions obtaining at the limit of the range of sugar maple, together with stand and stocking relations vary widely. Along the seaward approaches to the plateau the limit of the range of the species occurs at elevations of the order of 800 feet, that is, on the middle and lower flanks of the escarpment. As noted previously, upon passing upward toward the surface of the plateau the density of sugar maple is variable and frequently low, particularly in second growth stands, and on seaward slopes the limit of the range is delineated by scattered and well separated trees. In an altitudinal sense, however, the limit is abrupt. There is no gradual transition in size toward a depauperate form, or a marked decrease in vigor upon approaching the limit. On the contrary the individual sugar maple stems on the periphery of the range are commonly co-dominants comparable in size to other trees in the overstorey.

Conditions at the limit of the range in old growth stands were investigated on the steep sides of the valleys of the Grande Anse and Aspy Rivers. Here the altitudinal limit is of the order of 1250 feet, that is, on the upper reaches of the flanks of the plateau. In some sections of this area co-dominant, scattered trees mark the limit of the range. Reproduction of sugar maple is scanty and confined to

the immediate vicinity of seed bearing co-dominants. In topographically difficult areas, the density of sugar maple may be very low and the limit of the range consequently poorly defined. In one case, on an extremely steep and exposed southeasterly slope above the Aspy River, characterized by a very unthrifty growth of hardwoods not forming a closed stand, the limit of the range of the species is marked by seedlings growing well above the "furthest on" position of the scattered members of the overstorey.

TABLE IV.—Structure of upland, hardwood stands in northern Cape Breton Island

D.B.H.	Plot No. 4		Plot No. 5		Plot No. 6	
	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species
3	2	3	1	2	1	2
4	2	2	1	2	..	12
5	..	1	1	2	1	7
6	2	2	2	2	..	5
7	2	2	..	2	1	4
8	1	2	4	4	..	4
9	1	2	5	5	1	5
10	4	4	1	2	1	3
11	7	10	1	2	1	4
12	2	2	..	..	1	3
13	1	1	1	2	..	..
14	1	1	1	1	..	4
15	..	..	..	3	..	2
16	..	..	..	..	..	1
17	1	2	..	1	..	..
18			..	..	..	..
19			..	2	..	..
20			..	1	..	..
21			..	..	..	1
22			..	1	..	..
23			..	1	..	1
24			..	..		
25			..	..		
..						
..						
48			..	1		
Age (yrs.)	110		160		110	
No. of trees per acre	130	175	90	180	35	290
Basal area per acre (sq. ft.)	70	102	37	199	14	139

At inland stations a rather different situation obtains. Here the limit of the range is found on the more leisurely slopes of the upper reaches of the plateau. Under these circumstances sugar maple occurs not as widely-separated, individual trees but usually in mixed-wood stands (Table IV). Again, individuals on the limit are co-dominant, usually thrifty trees. Reproduction of the species is scanty and occurs in close proximity to seed-bearing members of the overstorey.

Preliminary observations indicate that germinable seed is produced in quantity on the limit of the range, but reproduction is scanty, with seedlings distributed in close proximity to the seed-bearing members of the overstorey. At present there is no suggestion of a wide age class distribution in seedlings. Rather, the size and occurrence of reproduction serves to maintain the abruptness of the limit of the range of the species.

Stand characteristics frequently are best considered within the framework of the technical forester's yield table, and this practice has been adopted in the present instance. We have been extremely fortunate in this regard in that Mr. S. J. Kostjukovits of the Department of Lands and Forests, Province of Nova Scotia, has most generously made available to us his unpublished compilations of growth and yield in hardwoods in the Province. In the present study appeal has been made also to the data of Gevorkiantz and Duerr (1937) and

TABLE V.—Stand and stocking relations in hardwood forests in northern Cape Breton Island

Plot	Location	Age	Ht. of av. Co-dom. tree	Trees per acre	Basal area (sq. ft./- acre)	Site-quality (A) ¹	(B) ²
A	Bottom- land	65	66	375	142	2	1
B	Upland	190	42	245	144	5	3
C	Lower slopes	85	64	385	151	3	2
D	Upland	160	43	180	199	5	1
E	Upland (limit of range)	110	46	290	139	5	3
G	Upland	110	39	175	102	5	5
I	Upland	90	43	340	153	5	2
J	Upland	90	43	340	128	5	3
K	Lower slopes	90	72	425	172	3	1
L	Bottom- land	110	64	420	173	4	1
N	Upland (limit of range)	85	45	210	150	5	2

¹ Based on height-age relations.

² Based on basal area per acre.

Hawes and Chandler (1914). A synthesis of observations made in a number of plots on a variety of sites is presented in Table V.

DISCUSSION

Reference to Table V indicates that site determination based on height-age relations leads to the inclusion of all upland plots in sites of poor quality (sites 4 and 5). On the contrary, a classification based on age, density, and dominance (basal area) results in the assignment of much superior site quality values. Clearly the height of the average co-dominant trees on upland sites in Cape Breton deviates markedly from normal. Possibly wind is involved here.²

Perhaps the most striking feature of the results gained in the present study is the demonstration of the abrupt nature of the "line" which marks the limit of the range of sugar maple in Cape Breton Island. Almost invariably the limiting trees are co-dominant members of the stand, approaching or equalling, both in height and diameter, the dimensions of trees of other species represented in the overstorey. This situation obtains on all types of topography, although the actual elevation of the limit and the degree of slope may vary widely. Similarly, as noted previously, the density and dominance of sugar maple on the limit of the range varies considerably.

In areas of uniform terrain, for example interfluves on the more leisurely upper slopes of the plateau at inland locations, there is not an uncommonly wide change in azimuth from tree to tree along the limit. However, topographic features deriving from any cause, and particularly water courses and exposed ridges, may be marked by considerable differences in the elevation of the limit, and by pronounced changes in form and stocking.

Wulff (1950) and Braun (1950) indicate that the range of a species is limited by the interrelations of a complex of factors, and their view is rather well supported by circumstances attending the limit of the range of sugar maple in Cape Breton Island. It is very difficult to demonstrate coincidences between the limit of the range of sugar maple and individual soil and associated topographic factors. In this regard it is of interest to recall the homogeneous nature of the rocks from which the soils of the region have been derived.

The situation is ostensibly the same with respect to meteorological considerations (see also Dansereau, 1957 in this regard). However, marked changes in the size, form and habit of individual stems in

² In this regard it is of interest to note that an analysis of storm track data presented in the Monthly Weather Review of the United States Weather Bureau indicates that in the interval 1939-1959 inclusive, approximately 2455 cyclonic centers moved across longitude 61° W., north of latitude 20° N. Of this total 2080 centers (85%) passed across the above meridian between latitude 30° N. and 60° N. The average latitude of passage of the centers across the meridian of 61° W. was 47° N. Further information bearing on the frequency and intensity of storms in the region of Cape Breton Island may be found in Volume One of the United States Navy's "Marine Atlas of the World."

bottomlands and at higher elevations point strongly to the possibilities of a climatic influence. Similarly, the wide differences in the elevation of the limit of the species on seaward versus inland slopes constitute presumptive evidence that meteorological factors are of significance in the distributional pattern of the species in Cape Breton Island.

The forests of Cape Breton, with the possible exception of the pure fir stands of the upland, have been included within the hemlock, white pine, northern hardwoods association of Nichols (1935); see also Braun (1950). In Braun's view, the vegetation of the hemlock-white pine-northern hardwoods region derives from post-Wisconsin migrations "which brought about an expansion from the unglaciated Allegheny Plateau and northern Allegheny Mountains without pronounced modification of type. The climax elements are almost entirely a result of these expanding migrations." Several species attain the limit of their ranges within this region, and Braun suggests that with further development of topography and soils, maple, beech, and hemlock may move farther north.

It is difficult on the basis of present evidence to decide whether the limit of the range of sugar maple in northern Cape Breton is now stationary, advancing, or retreating. Application of the criteria of Griggs (1946) regarding advancing timber lines leads to inconclusive results. Likewise, age class distribution patterns in reproduction and overstorey do not suggest any particular trend.

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Interaction of Natality, Mortality and Movement during One Annual Cycle in a *Microtus* Population

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ABSTRACT: A population of meadow mice, *Microtus pennsylvanicus*, was studied through one annual cycle, near East Lansing, Michigan. In May the mice were at a very low density and living under good conditions of food and cover and experiencing little competition. Because of high natality the population increased rapidly throughout the summer and fall. Breeding ceased in January, and the population continued to increase in February as a result of immigration. Mortality was highest in the summer and least in the winter. This was the result of (1) change in the age composition of the population, and (2) probable reduction of predation due to a persistent snow cover. A life table showed that mortality was highest in the postnestling juveniles and young adults. In other age classes mortality continued at approximately 50 per cent. The natural rate of increase of the population was -0.0315 daughters per female per day. Although the rate of increase was negative, immigration was sufficient to cause the population to increase in size.

Although the population dynamics of meadow mice of the genus *Microtus* has been the subject of considerable research both in North America and Europe, our knowledge of the interaction of mortality, natality, and movement in a single population of this genus is still far from complete. In this paper I intend to present a detailed analysis of these factors in a population of *Microtus pennsylvanicus*. The data for this analysis were obtained during an intensive one and one-half year investigation of the energy flow through an old-field vegetation — *Microtus pennsylvanicus* — *Mustela rixosa* food chain. (Golley, 1960).

My studies were made in 1956 and 1957 in an abandoned field near the Michigan State University campus, East Lansing, Michigan. Blue grass (*Poa compressa*), wild carrot (*Dauca carota*) and Canada thistle (*Cirsium arvense*) were the chief dominants in the vegetation. Since occasional burning was the only disturbance to the vegetation for about 15 years prior to the study, a dense sod of grasses and perennial herbs had developed and provided an abundance of cover and food for the meadow mice. During the study period the weather was unusually mild. The temperature was above average in every month except September, 1956, and January, 1957, and precipitation was below average throughout the fall and winter. The study area was surrounded on four sides by orchards, alfalfa fields, and old-field vegetation, all of which furnished habitat for *Microtus*.

Acknowledgments.—I am grateful to Dr. Don W. Hayne, Fish and Wildlife Service, for his advice on methodology and analysis of the data on density, natality and mortality. I am also grateful to Dr. Helmut K. Buechner, Dr.

Richard A. Parker, Washington State University, and Dr. Eugene P. Odum, University of Georgia for their comments on the manuscript. Dr. Parker kindly pointed out errors in my calculation of expectation of life and natural rate of increase. However, any errors in computation or interpretation are my own responsibility.

METHODS

Population density, natality, and mortality were determined by a mark and recapture technique using a modified Sherman live-trap, with a wooden floor and hardware cloth end-wall and door. Mortality of mice within the traps was kept at a low level by covering the traps with aluminum foil-covered-asphalt shingles. The traps were baited with oatmeal. The trapping pattern was devised by Hayne (1959) and is described in Golley (1960). Briefly, the pattern consisted of two cross lines 100 meters in length, of 50 traps each. These lines were operated alternately for 24 hours, for a total of 6 days, resulting in three days of trapping for each line. The ratio, number of individuals captured in common by both lines divided by the average capture per line, provided an estimate of the fraction the average capture per line was of the total population. This technique was tested in an isolated field by Hayne and Golley (unpublished) by using the cross-line trapping pattern to provide a population estimate and then checking the estimate by removing all the mice in the area with snap traps. The population estimated obtained by the two methods were nearly the same (217 and 225 per acre).

Each newly captured animal was marked by toe clipping, and weighed, sexed, and examined for reproductive condition. Pregnancy was determined by palpation of the abdomen. On subsequent captures the animal was weighed and again examined for pregnancy. The age of the specimens was determined by converting live weight to age in days, using Hamilton's (1937) growth curves for *Microtus pennsylvanicus*. Although Whitmoyer (1957), in a study of growth rate of laboratory-raised *Microtus pennsylvanicus*, concluded that weight was only a general criterion of age, the age-weight conversion is used here for lack of a more exact field criterion.

Natality was determined from knowledge of the percentage of females found to be pregnant, the known gestation period for the species (21 days) and the average litter size in snap-trapped specimens taken in similar habitat at the same time of the year (5 young per litter). The number of days for an average female in the population to give birth to a litter was estimated by dividing the gestation period by the per cent pregnancy (termed f). Every $21/f$ days an average female would produce a litter of 5 young, of which 2.5 were females. Thus in the time interval, $21/f$ days, one female would increase to 3.5 females. With this information the following formula was used to calculate natality:

$$\frac{\log_e 3.5}{\frac{21}{f}} \times t \times p \quad 1.$$

where f is the per cent pregnant females, t is the time interval between trapping periods, and p is the mean population.

Mortality equalled the disappearance of individual mice from one period to another, assuming that all the animals in contact with the line were captured at each period. This assumption is nearly correct since only 14 of approximately 500 mice were not taken in every consecutive trapping period from the first to the final period in which they were captured. For any one trapping period, only 10 per cent of the new captures were made in the last two days of trapping; this is further indication that the 6 days was adequate to capture the population in contact with the lines.

Although, the cross-line trapping pattern could not be used to estimate the home range of the mice, an index of movement could be calculated by averaging the distances each animal moved between captures in one trapping period, assuming a straight-line movement from one trap to the next. This index of movement does not tell how far an animal actually moved, but is an indication of the movement activity of the animals during a trapping period.

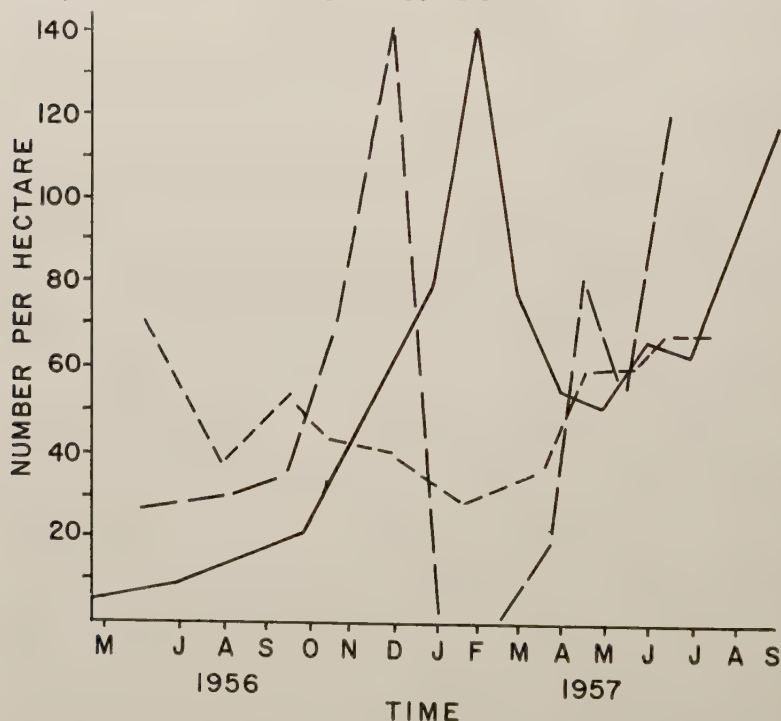


Fig. 1.—Density (solid line), natality (long dash line) and mortality (short dash line) of *Microtus* during 1956 and 1957 in southern Michigan. Natality and mortality are shown as the number of births or deaths per hectare per month.

RESULTS

At the beginning of the investigation practically no animals were present on the study area. The population exhibited an extremely rapid rate of increase (Fig. 1) during the first summer and fall, the rate being almost a doubling of the population every two months. This increase did not continue throughout the year. A reduction in the population occurred in mid-winter, and a second increase began the following spring.

Birth of mice per hectare per month (Fig. 1) increased throughout the spring and summer to a peak in December. Breeding stopped during winter; pregnant females were not found in January, or February, and the pregnancy rate was low in March (11%). Hamilton (1941) also found that *Microtus pennsylvanicus* in New York stopped breeding during the winter, except when the population density was extremely high.

Mortality trends (Fig. 1) were somewhat different than those expected. It was anticipated that in the winter cold rains and heavy snow-fall might cause greater mortality in the population, but this does not appear to have been the case. As shown in Fig. 1, mortality was highest during the summer and decreased to a low in mid-winter. The average mortality for each age-class was considered in a life table (Table I). Highest mortality (61% and 58%) occurred in the post-nestling juveniles (11 to 20 grams) and young adults (21 to 30 grams). In other age groups mortality was about 50 per cent.

Since the population of *Microtus pennsylvanicus* was living under near optimum conditions, the natural rate of increase of the population (r) might be expected to approach the innate capacity for increase of the species. The innate capacity for increase, as defined by Andrewartha and Birch (1954), is the maximal rate of increase when quantity of food, space, and other animals of the same kind are kept at the optimum. Following the methods of Birch (1948), a female life table and age specific fecundity table were prepared (Table II). This fecundity table is age specific because the pregnancy rate does vary with age; however, the number of young per litter which might be

Table I.—Life table for the population of male and female
Microtus pennsylvanicus

Weight Class x	Days	No. surv. at beginning of age period of 100 l_x	No. dying in interval d_x	Mortality rate/100 $100q_x$	Expectation of life e_x
0-10	0-10	100.0	50.0	50.0	11.4
11-20	11-21	50.0	30.5	61.0	15.2
21-30	22-33	19.5	11.3	58.0	19.5
31-40	34-54	8.2	4.3	52.5	27.0
41-50	54-103	3.9	2.1	53.9	31.8
51+	104+	1.8	1.8	100.0	12.8

TABLE II.—Life table and age specific fecundity table for female *Microtus*

Midpoint of age-class days x	Days between age-periods t	Total no. ♀	No. surv. to next period	Prob. of ♀ being alive at beginning of period l _x	% pregnant	$\frac{21^1}{f}$	$\left(\frac{\text{nat. log. } 3.5}{\frac{21}{f} m_x} \right)$	$\frac{l_x m_x}{x n l_x}$
5.0	—	2	1	1.000	0.00	—	.0000	
16.0	11	50	14	.500	.21	100.0	.1378	.0689 1.1024
27.5	12	103	73	.140	.54	38.9	.3865	.0541 1.4880
44.0	21	73	21	.099	.59	35.5	.7411	.0734 3.2283
79.0	49	17	6	.029	.80	26.2	2.3430	.0649 5.3681
104.0	—	1	1	.010	0.00		.0000	
								$R_0 =$
								.2643 11.1868

$$T = \frac{11.1868}{.2643} = 42.33 \text{ days} \quad r = \frac{-1.3318}{42.33} = -0.0315$$

1 Gestation period/percent pregnancy.

age specific is held constant at 5. The net reproductive rate (R_0) indicated that this population would multiply 0.264 times per generation. The mean generation time was approximated by the formula:

$$T = \frac{x l_x m_x}{l_x m_x} \quad 2.$$

where T is the mean generation time, and x , l_x , and m_x are taken from the female life table. The mean generation time was 42.33 days. With this information the natural rate of increase (r) was estimated as:

$$r = \frac{\log_e R_0}{T} = \frac{\log_e 0.2643}{42.33} = -0.0315 \text{ daughters/♀/day} \quad 3.$$

This means that at any instant the death rate is greater than the birth rate.

The movement index (Table III) showed some interesting fluctuations. Although males and females appear to have approximately the same average movement index when the entire year is considered, during the spring and summer the males show greater movement than the females. The females when relieved of maternal duties during the winter move about more than the males. Total movement during the winter for both males and females was less than during other seasons.

DISCUSSION

The aim of this report is to explain the observed changes in numbers of meadow mice by considering the interaction of natality, mortality and movement. Natality increased during the spring, summer and fall, until January when all reproductive activity ceased. The reason for a winter cessation of breeding in *Microtus* is not completely known. Baker and Ranson (1932) showed that *Microtus agrestis* required a light ration of 15 hours light per day to breed in the labora-

TABLE III.—Seasonal movement and mortality of male and female *Microtus*

Average Movement in Meters			
Season	♂	♀	Both Sexes
September to December	16.5	16.1	16.2
January to March	8.3	16.0	9.1
April to June	12.9	9.7	11.4
July to September	17.7	9.1	14.3
Average	13.5	13.1	12.8
Average Per Cent Mortality Per Month			
Season	♂	♀	Both Sexes
September to December	51	39	47
January to March	28	38	31
April to June	61	65	64
July to September	67	56	64
Average	47	48	47

tory. Whitmoyer (1957) also observed this to be true for *Microtus pennsylvanicus*. However, in this field study there appears to be only slight correspondence between breeding and light, when light is represented by the hours of sunshine recorded by the East Lansing weather station and hours of light between sunrise and sunset, taken from the Tide Tables, 1957-1958. Natality reached a peak in December (Fig. 1) which was the period of minimum light. Since Hamilton (1941) reported winter breeding during high population densities, probably factors other than light are also important in regulating breeding in this species.

Reduction in mouse density during the winter was due to the cessation of breeding associated with a continuing mortality. However, mortality was lower in winter than during the spring or summer (Table III). Probably this depression of winter mortality rates was largely due to a change in the age composition of the population. As shown in the population life table (Table I), the mortality rate was highest for the 11 to 20 gram weight class. Since these animals and the nestling young were not present in the winter population, the mortality would be less than when these ages were present. The oldest mice also decreased during the winter period, with the result that the late winter population was made up mainly of 21 to 40 gram animals.

Reduction of predation, especially avian predation, due to persistent snow cover may also have contributed to low winter mortality rates; however, quantitative data on this point are not available. Snow was on the ground for 28 days in January and 23 days in February, 1957 (East Lansing Weather Bureau, Local Climatological Data). Although, *Microtus* dug through and ran for short distances on top of the crust, a myriad of tunnels and runways were concealed beneath the snow. No signs of avian predation on *Microtus* were noted during the winter period.

There appears to be a correspondence between the amount of movement (as indicated by the movement index) and mortality in both sexes (Table III), especially in winter when movement and mortality both decrease. Although this correspondence is not unreasonable, since the probability of having an accident or of contacting a predator might be expected to be greater as the animals move about more, the correlation of movement on mortality for both sexes is not significant ($r = 0.089$). Movement may be an influence on mortality, but other factors seem more important in this particular situation.

Increase in the population during the spring and summer was due to production of new mice by the resident population. In January, when there was no reproductive activity, the population continued to increase and reached a peak of about 140 mice per hectare. This late season increase resulted from immigration of mice into the study area. The study area was located in optimum habitat and mice living on the adjacent exposed hillsides where the vegetation was less dense apparently moved into the dense lowland sward of grasses and herbs.

Throughout January and February there was an increase in capture of unmarked mice immediately before or during snow storms associated with an increase in the incidence of capture of the resident mice. This increase was interpreted to mean that the mice in some way anticipated storms and moved into more favorable habitat for the storm period and possibly for the entire winter.

The negative rate of natural increase (Table II) may also be explained by the immigration of mice into the population. The life table was calculated from all mice appearing in the population throughout the year, and included immigrant mice which did not reproduce while in the population. The increase in numbers of mice over the year is the result of both natality and immigration. Although the death rate at any instant was larger than the birth rate, immigration was sufficient to cause the population to increase in size.

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Responses of Small Mammals to Live-traps and Weather Conditions

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ABSTRACT: A comparison was made between the responses to live-traps of marked and unmarked individuals of *Microtus pennsylvanicus* and *Peromyscus leucopus*. Previously captured individuals of *M. pennsylvanicus* were more readily captured than were the unmarked ones, even after an interval of a month. There was no difference in the rates of capture of marked and unmarked *P. leucopus*. Comparisons of a given live-trapping technique utilized in two different habitats (marsh and old field) indicated no significant difference in its effectiveness after the second day of trapping. *M. pennsylvanicus*, in an old field, was found to abandon diurnal activity in favor of nocturnal and/or crepuscular activity when the temperature rose above 20°C. During the winter, when the temperature dropped below 0°C, activity was much less at all times. Except for less activity during the days the temperature rose above 20°C, such responses were not observed in the marsh. *Blarina brevicauda* was found to be more active on cloudy days than on those that were sunny or rainy. No correlations between activity and temperature variations was observed for this species.

Estimates of population densities of small mammals are normally derived from trapping data. The results depend upon a variety of factors in addition to the actual abundance of the mammals. Variations in responses to traps, positioning of the traps, home range size, amount of movement within the population, and weather conditions influence the estimates of population densities (Sealander and James, 1958; Goodnight and Koestner, 1942; Hayne, 1950; Calhoun and Casby, 1958; Getz, 1961a).

Responses to traps are particularly important. A method widely used in determining population densities from trapping data is the proportional method ("Lincoln Index" or modifications thereof; Hayne, 1949). A basic assumption involved in this method is that the probability of capture of the marked animals is the same as that of the unmarked animals. Morris (1955) and Chitty and Kempson (1949) found that marked individuals entered traps more readily than did those that had not been captured previously. Tanaka (1956) found the same to be true of certain species, while in others the probability of capture decreased after the initial capture. He further found that some may be "isoresponsive." Leslie (1952) assumed the marked and unmarked individuals to be captured with equal facility, although prebaiting was utilized to overcome any initial reluctance of individuals to enter traps (this initial reluctance has been discussed by Sealander, *et al.*, 1958).

Responses to weather conditions also influence estimates of population densities, particularly those sampled by means of snap-back traps. Burt (1940), Gentry and Odum (1957), Pearson (1959, 1960)

and Benton (1955) have discussed the responses of small mammals to weather conditions. There is still much to be learned, however, concerning the influence of weather upon the activity of small mammals.

The present paper deals with the meadow vole, *Microtus pennsylvanicus*, the white-footed mouse, *Peromyscus leucopus*, and the shorttail shrew, *Blarina brevicauda*. The data concerning *Microtus* and *Blarina* were compiled from a study of small mammal distributions in southern Michigan (Getz, 1959); those pertaining to *Peromyscus* were taken from Burt's study of small mammal populations on the Edwin S. George Reserve, 1935 to 1937. The *Microtus* and *Peromyscus* data were obtained from captures while those of *Blarina* were obtained primarily from signs.

I wish to thank Dr. W. H. Burt for making available to me the data concerning *Peromyscus*. My wife, Mary Ruth, made many of the compilations of the *Microtus* data.

STUDY AREAS

Data were obtained from three habitats, an abandoned field ("old field"), a grass-sedge marsh, and an oak-hickory wood lot, all located in southeastern Michigan. I have described the first two habitats elsewhere (Getz, 1961b). In brief, the old field supports a sparse stand of *Poa compressa* (65 gr/M²) with a few scattered forbs (*Daucus Carota*, *Solidago* spp., and *Potentilla intermedia*). The soil is relatively dry throughout most of the year. The marsh supports a dense stand of grasses and sedges (325 gr/M²). From October to June the surface is inundated in most places; when not inundated, the substrate is almost completely saturated. In comparison with the old field, the marsh is the more favorable vole habitat (Getz, *op. cit.*). The data pertaining to *Peromyscus* were obtained from an oak-hickory wood lot. For a description of this habitat see Burt (1940).

METHODS

TRAPPING

The entire old field (2.5 hectares) and a 4.4 hectare portion of the marsh were grided with a 12-meter interval. The stations so established were trapped for five days each month September, 1957, through September, 1958. Because of the large number of stations in the marsh, two trapping periods were required to cover all stations. For the first four days of a trapping period the traps were checked twice a day, 0800 to 1100 and 1600 to 1800. On the fifth day the traps were checked only in the morning, at which time they were picked up and moved in preparation for the next trapping period. Wooden multiple-catch traps of the type described by Burt (1940) were employed throughout the study. Bait consisted of equal amounts of sunflower seeds and commercial chicken scratch (cracked

corn, wheat, oats, millet, and buckwheat). No prebaiting as such was employed. Traps were placed at the stations at least one day in advance of a trapping period (upside down, with the doors open). The traps normally contained bait from the previous period, which may have served as prebaiting. Individuals were marked by toe clipping.

The traps utilized were not efficient in holding *Blarina* since most of the shrews were able to open the trap-door and escape. As a result few actual captures were recorded. From the odor and feces in the trap, however, it was possible to determine that a trap had been entered by this species. Much information in the form of signs, therefore, was obtained concerning *Blarina*.

Burt used the same type of trap, positioned in a slightly larger grid (13.5-meter interval). Since he was studying a nocturnal species, his traps were normally checked only in the mornings. The trapping periods were six days long with an interval of one week between periods. Hemp seeds were used as bait. No prebaiting was employed in the study. The individuals were marked by a combination of ear punching and toe clipping.

ENVIRONMENTAL FACTORS

A dial maximum-minimum thermometer (U.S. Weather Bureau type) was placed in the old field and marsh to record temperatures at the level of the vole runways. During the period of June through September a second thermometer was placed in a site in the old field where the vegetation was more sparse than at the permanent station. Readings were made each time the traps were checked.

A record was made each day as to the weather conditions. In the analysis of the data, a day was considered to be cloudy if the sun was covered for more than half of the day. A day was considered to be "rainy" if any rain at all fell. Data concerning rainfall and intensity of moonlight were not recorded during the night. Burt kept general notes as to whether the night had been clear, cloudy, or rainy. He has discussed the influence of weather upon the activity of *P. leucopus* elsewhere (Burt, 1940).

RESULTS

RESPONSE TO TRAPS

Time to capture the known population.—In making comparisons of population densities of a species in different habitats, one must assume that the trapping technique employed is equally effective in all or make allowances for any differences. Since the marsh and old field differed markedly in environmental conditions, the *Microtus* data have been analyzed to determine the relative effectiveness of the trapping technique used in the study in these two areas.

One cannot always be certain that the entire population of an area has been trapped; certain individuals may avoid the traps and

never be captured (Pearson, 1959). Because of this, it is necessary to use the known population (i.e., those individuals known to be present) to determine the rate at which the population was captured in each area. Thus, while a lesser percentage of the population was captured initially in the old field, by the afternoon of the second day approximately the same percentage of the known population was captured in both areas (Fig. 1). There is no significant difference in the rate of capture from the second through the fifth day. Likewise, there is no significant difference between the areas in regard to the individuals known to be present, but not captured a given period (3 and 4% for the marsh and old field, respectively).

Comparison of unmarked and marked individuals.—*Microtus*: As stated above, the marsh was trapped in two periods each month,

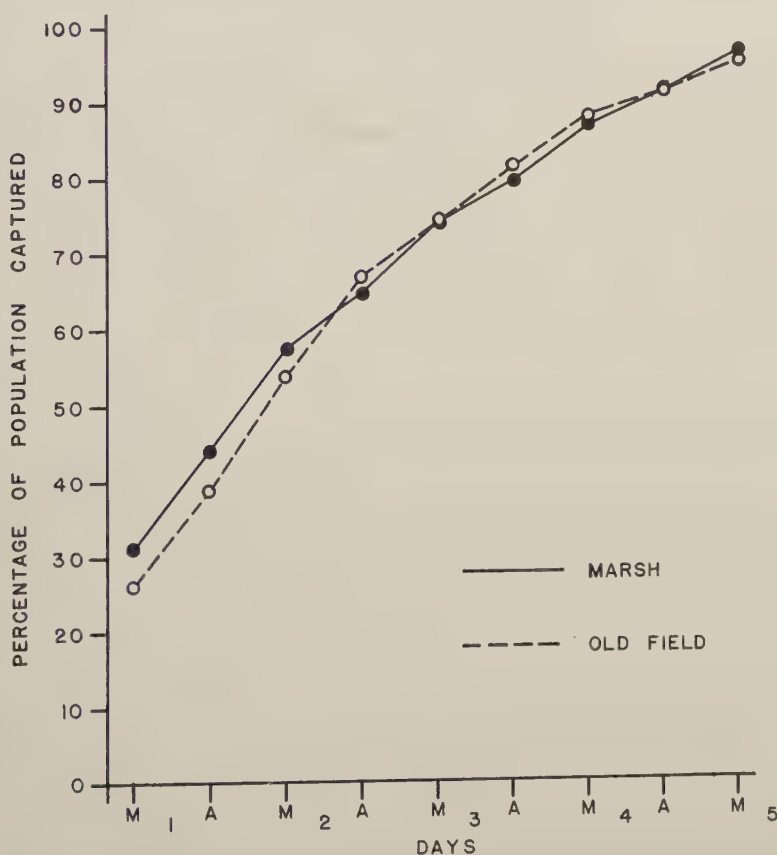


Fig. 1.—Rates of capture (live-trap) of the known population of *Microtus pennsylvanicus* in marsh and old field habitats; based on 13 trapping periods in each habitat. M, morning check of traps; A, afternoon check.

about half of the study area being trapped each period. Those individuals whose home ranges were on the boundary between the two sections were often captured during both periods. Since comparisons of unmarked individuals with those marked the previous month were desired, inclusion of these animals in the analysis of the recaptures would bias the results. To avoid this bias, only data from the first period of each month have been included in the discussion of recaptures in the marsh.

The unmarked individuals appearing on an area represent individuals immigrating or leaving the nest since the last trapping period. Such processes occur continuously and thus are taking place during a trapping period. If one considered all the new individuals caught a given month to have been present the first day of trapping, estimates of the percentage captured each day would be biased (too

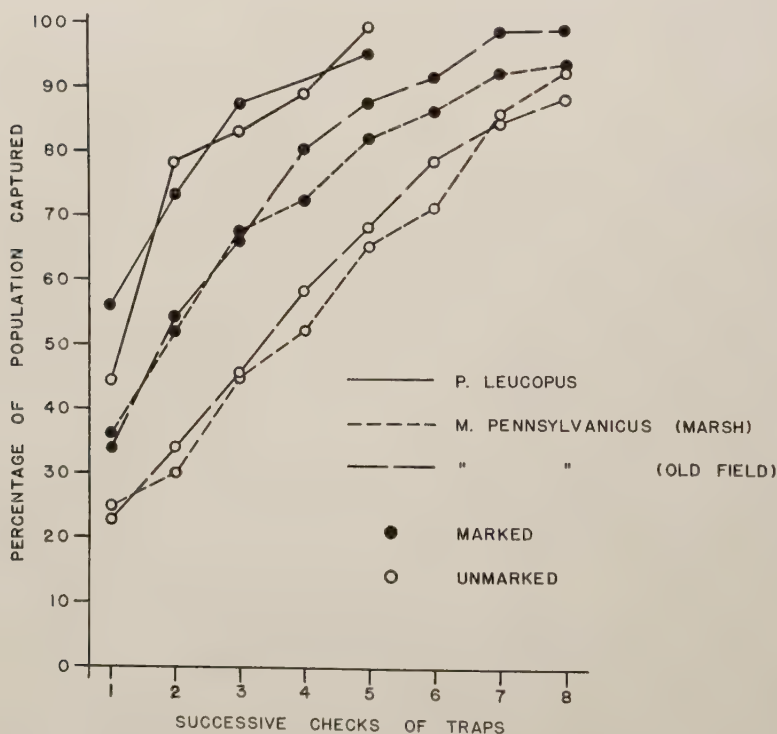


Fig. 2.—Rates of capture of marked and unmarked individuals of *Peromyscus leucopus* and *Microtus pennsylvanicus*. Traps for *P. leucopus* were checked once a day, in the morning; those for *M. pennsylvanicus* twice a day, morning and afternoon. *P. leucopus* data based on 5 trapping periods; *M. pennsylvanicus* data based on 13 trapping periods in each habitat.

low). To avoid this bias, the average number of new individuals appearing on an area each day was computed. In determining the rate of capture of the unmarked individuals, only the number predicted to have appeared by the time of each trap-check has been used in calculating the percentage captured.

Comparisons of rates of capture of the two groups of individuals

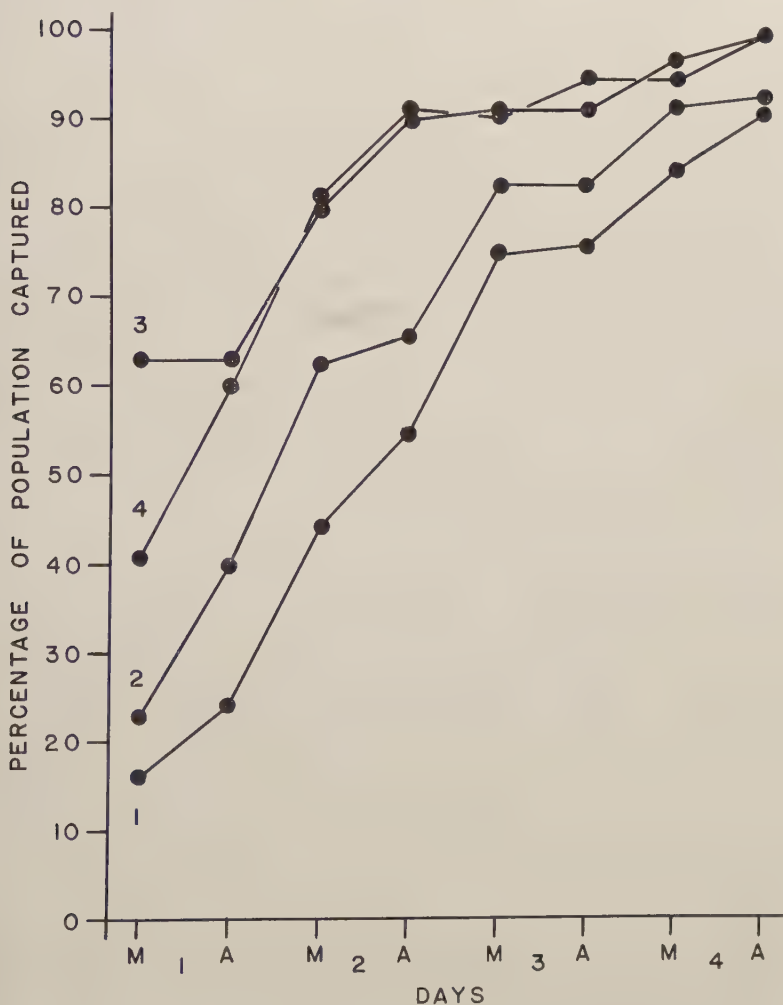


Fig. 3.—Initial rate of capture (1) and rates of capture for subsequent 3 months (2-4) for individuals of *Microtus pennsylvanicus* first captured in June, 1958. The number of individuals included in each sample are 54, 30, 30, and 21 for 1 through 4, respectively.

clearly show that the individuals marked the previous month were captured more readily than were the unmarked animals (Fig. 2). This was true during all months in both areas except for the month of April in the marsh. During this month, the rate of capture of unmarked individuals was slightly greater than that for the marked ones.

It was also desired to determine if the rates of capture became greater during subsequent trapping periods (i.e., with more exposure to traps). To do this, the recapture data for the individuals first captured a given month were studied to see if those individuals that survived were recaptured more readily the more periods they remained on the area. The data for most months indicate that the rate of capture increased up to the third period. Since the average survival time of *M. pennsylvanicus* was less than three months (Getz, 1960), insufficient data were available to determine rates of capture after the third month. Data for the group with the best survival is given in Figure 3.

Peromyscus.—Only five trapping periods were found to have enough unmarked individuals appearing between periods to allow comparisons between the responses of marked and unmarked individuals. These data show that unlike *M. pennsylvanicus*, the individuals captured the previous trapping period were not more readily captured than were the unmarked individuals (Fig. 2). Tanaka (1956), utilizing part of Burt's data in a different manner, also found *P. leucopus* to be isoresponsive.

RESPONSE TO WEATHER CONDITIONS

Microtus.—Hamilton (1937) has shown *M. pennsylvanicus* to be primarily crepuscular and diurnal in habits. During the present study the traps were checked after dawn and just before dusk. The captures recorded in the morning, therefore, represent those individuals that entered the traps during the two peaks of crepuscular activity as well as during the night. Those captures recorded in the after-

TABLE I.—Influence of weather upon the activity of *Microtus pennsylvanicus* (based on 5369 and 1043 captures in the marsh and old field, respectively)

Weather	Percentage of population caught			
	Marsh		Old field	
	Day	Night	Day	Night
Rainy	14		20	
Cloudy	21		20	
Sunny	19		21	
Above 20° C	12	33	10	41
Below 0° C	21	41	8	17
Average (all conditions)	19	36	19	34

noon check of the traps, however, represent individuals active during the day. This facilitates comparison of the captures with daytime weather conditions.

There was no difference in the captures on cloudy days in comparison with sunny days (Table I). This was true in the old field, where the vegetation was sparse, as well as in the marsh which had much more cover. In the marsh there were slightly fewer captures those days during which it rained than on days that no rain fell. No difference was evident in the old field.

The most obvious influence of temperature upon the activity of the voles was observed in the old field. During the summer when the temperature was above 20° C there were fewer captures during the day and more at other times (Table I). Apparently, when daytime temperatures become extremely high, diurnal activity is abandoned in favor of increased nocturnal and/or crepuscular activity.

During the winter when the temperatures dropped below 0° C, captures were fewer in the old field both during the day and night. This was especially true of January and February. During January and February, 62 and 89 per cent, respectively, of the known population was not captured. That these individuals were resident on the area was indicated by the presence of surface nests after a cover of snow had melted. Presumably their activities were restricted to such an extent that they did not range far enough to encounter traps.

Data from the marsh also indicate that the voles are less active on days during which the temperature rises above 20° C. The nocturnal and crepuscular activity under such conditions was also slightly less, however. There was no decrease in the numbers of captures in the marsh on days or nights during which the temperature dropped below 0° C. There were actually slightly more captures during such nights.

The more extreme temperatures in parts of the old field may contribute to the difference in responses in the two areas. The thermometer in the more exposed part of the field (and where the voles were most abundant) indicated especially high daytime temperatures in the summer (7 to 10° C above those in the marsh). Winter temperatures were also probably more extreme (temperatures were obtained only during the months of June through September). Although 20 and 0° C have been used as delimiting temperatures for comparing amounts of activity in both areas, the temperatures

TABLE II.—Influence of weather upon the diurnal activity of *Blarina brevicauda* in a grass-sedge marsh (data compiled from entire study)

Weather	No. signs during day	No. signs previous night	Relative amount diurnal activity
Sunny	168	279	60%
Cloudy	108	101	107%
Rainy	183	263	70%

in the old field were more extreme. A greater modification of the activity pattern, therefore, resulted.

Blarina.—The data concerning *B. brevicauda* involve the use of signs rather than actual captures and cannot be analyzed in the same manner as were the *M. pennsylvanicus* data. Since shrews prefer a cool, moist atmosphere (Pearson, 1959; Pruitt, 1959) nights would normally have more favorable atmospheric conditions than would days, especially during the summer. The relative amount of diurnal activity (number of signs recorded during the afternoon check of the traps divided by the number recorded during the morning check) has been used to determine the influence of sunshine and rain upon the activity of this species.

There were fewer signs in the marsh on sunny days than on those that were cloudy or rainy (Table II). Also there were fewer signs when it rained than when it was merely cloudy. Cloudy days appear particularly favorable as more signs were recorded during such days than the preceding nights. Less activity on sunny days may be a response to lower humidity conditions rather than to sunshine itself; humidity measurements were not obtained in the present study, however. During June through August daytime activity was less under all conditions than at other times of the year (sunny, 37; cloudy, 50; rainy, 67% of the crepuscular and nocturnal activity). The same general conclusions appear to apply to the old field. This area was too dry to support a large population of shrews throughout the year (Getz, 1961c). As a result there were too few data for analysis.

Temperature variations had no marked influence upon the activity of *B. brevicauda* in the marsh. Signs were only slightly fewer (3 to 4% below average) on nights the temperature dropped below 0° C and on days it rose above 20° C. Temperature extremes may have combined with the dryness of the substrate to make the old field an unfavorable shrew habitat. The data were too few to determine the influence of temperature upon the activities of the short-tail shrew in this habitat.

DISCUSSION AND CONCLUSIONS

All species of small mammals do not respond in a similar manner to live-traps. In some species, the unmarked individuals are less readily captured than are the ones captured previously, in others the reverse is observed, while still others are isoresponsive. To accurately determine population densities from trapping data, one must, first determine the response of individuals of each species to the traps. The data involving those species not isoresponsive must then be corrected to obtain valid estimates of population densities.

Microtus pennsylvanicus was found to be similar to *M. montebelli* (Tanaka, 1956), *M. agrestis* (Chitty and Kempson, 1949), *Peromyscus maniculatus*, and *Clethrionomys gapperi* (Morris, 1955) in that marked individuals were more easily captured, even after an in-

terval of a month, than were the unmarked individuals. Unmarked individuals of *Peromyscus leucopus*, on the other hand, were captured as readily as were the marked ones.

Responses to weather conditions also vary. In the present study *Blarina brevicauda* was found to be less active on sunny days while *M. pennsylvanicus* was just as active on such days as it was on cloudy days. Furthermore, the activity of *M. pennsylvanicus* was influenced by temperature variations. The responses of each species to the weather conditions occurring during a trapping period must, therefore, be determined and compensated for in obtaining estimates of population densities (this would apply particularly to short period snap-trapping).

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Plants of Fargo, North Dakota¹

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ABSTRACT: A list published in 1921 included 540 species and now 125 more are added. Some of these were overlooked before, many new weeds have been introduced and some cultivated plants have become established. About 20 species that did not occur naturally in the area, but did occur on higher ground a few miles distant, have become established in sand used as ballast for railroad tracks. Probably five or six species have disappeared and a dozen others are endangered by conversion of a wooded area into suburban homes. Other changes in status are noted. Only small remnants of prairie persist.

A list of the wild plants in the vicinity of Fargo, North Dakota and Moorhead, Minnesota was published (Stevens, 1921) which included 540 species. Since that date additional species have been introduced and some native plants have disappeared. The present supplement to that list records some 125 additional species that have been observed over the 40-year period. The names used here are those of Gray's Manual, 8th ed., and no note is made of changes from the previous list except for a few errors. Neither are flowering dates included here. Revised dates for weeds have been published (Stevens, 1956) and a complete list is in preparation.

The area included is approximately 10 miles in diameter. Only the Red River Valley is represented, with the river bank and its narrow fringe of trees, fields, roads and city environs. The soil is silt or clay with no natural sand or stones. Occasional drainage channels furnish a wetter habitat while the ridges of artificial drains and road grades provide drier places. If the area were extended to a 50 mile diameter it would include some of the sandy Sheyenne Delta to the southwest and higher ground beyond the valley to the east thus adding materially to the list of species.

The original prairie flora can be judged only from very small remnants in cemeteries and along roadways where invasion of immigrant species is often heavy. Timbered areas have suffered as much in recent years from pasturing and from urban developments. Increases in park areas have resulted in removal of undergrowth, development of playgrounds, etc. Edgewood Golf Course now occupies the largest river bend which was formerly one of our favorite places. A limited flora still persists on one edge but most if not all of the *Crataegus mollis* and *Populus tremuloides* have been removed. The one colony of *Solidago flexicaulis* persisted nicely until a few years ago.

On the Minnesota side of the river, northward from the above

¹ Contribution from North Dakota Institute for Regional Studies, Journal Series, Paper No. 11.

area, were many acres of *Populus tremuloides*. Much of this is now occupied by suburban homes and *Viola conspersa*, *Monotropa uniflora*, *Pyrola elliptica*, *Thalesia uniflora*, *Senecio aureus*, and *Petasites sagittata* are probably gone. Others that have been reduced and may be lost are: *Oryzopsis asperifolia*, *O. racemosa*, *Schizachne purpurascens*, *Uvularia sessilifolia*, *Smilacina racemosa*, *Anemone quinquefolia*, *Rubus pubescens*, *Desmodium glutinosum* and *Geranium maculatum*.

Recently introduced species are mostly accounted for in the present list. Roadsides have become less productive for collecting because of road widening, surfacing and occupation largely by *Bromus inermis*, *Melilotus* and *Lactuca scariola*. Chemical control of railroad edges has nearly eliminated one large source of new weeds.

One feature of special interest is the arrival of native species in the gravel ballast for railroads. Many that were not originally present appear occasionally and some have become well established. The recent use of crushed granite for ballast has tended to reduce this list. In 1938 the Northern Pacific Railway raised its tracks several feet for the Thirteenth Street subway. The sand used there shows a nice growth of *Equisetum hiemale*, *Sporobolus cryptandrus*, *Cyperus schweinitzii*, *Petalostemum purpureum* (present in prairie), *Lithospermum incisum* and *Helianthus petiolaris* as well as *Cenchrus longispinus*, *Stipa comata*, occasional *Astragalus striatus*, *Artemisia glauca*, the one *Prunus pumila* and other species.

LIST OF SPECIES

Juniperus virginiana L., Eastern Red Cedar.—Along the river near Fargo in 1959, J. R. Nelson. Doubtless a seedling from planted trees.

Typha angustifolia L., Narrow-leaved Cattail.—First noticed in 1958 but must have been here some years. It seems to be increasing rapidly.

Potamogeton foliosus Raf.—Roadside ditch in 1952.

P. zosteriformis Fern., Flatstem Pondweed.—Collected by L. R. Waldron in 1902.

Triglochin maritima L., Arrowgrass.—Occurs at Moorhead and Dilworth, Minnesota.

Poa annua L., Annual Bluegrass.—First noted in 1920 and has become rather common in moist and bare places in lawns and waste corners.

Glyceria borealis (Nash) Batch., Northern Mannagrass.—There is a specimen labeled Fargo, July 5, 1898. We have not seen it in recent years.

G. striata (Lam.) Hitchc., Fowl Meadowgrass.—Collected north of Moorhead in 1955.

Bromus ciliatus L.—No specimens at hand from Fargo but several from adjacent areas.

B. tectorum L., Downy Bromegrass.—Abundant by railway elevator in Moorhead in 1958.

Puccinellia nuttalliana (Schultes) Hitchc., Alkali Grass.—Occasional in wet, saline soil.

Agropyron cristatum (L.) Gaertn., Crested Wheatgrass.—First collected in 1937 on town lot.

Diplachne fascicularis (Lam.) Beauv.—Found in 1955 around a lumber yard; also in Moorhead in 1958.

Calamovilfa longifolia (Hook.) Scribn., Big Sandgrass.—Along railroad in 1923.

Buchloe dactyloides (Nutt.) Engelm., Buffalograss.—A small spot in native prairie, found in 1921, was soon destroyed by industrial developments.

Muhlenbergia asperifolia (Nees & Mey.) Parodi, Scratchgrass.—Low prairie by railroad.

M. richardsonis (Trin.) Rydb. Previously cited as *M. cuspidata* which does not occur in the area.

Setaria verticillata (L.), Bur Pigeongrass.—First noted in 1922, it has become frequent and quite a nuisance around gardens and neglected town lots.

Digitaria sanguinalis (L.) Scop., Common Crabgrass.—This has been found several times in recent years and gives some evidence of persisting.

Panicum perlongum Nash.—Has not been collected again and probably was destroyed at the original station.

P. wilcoxianum Vasey.—On railroad ballast in 1942.

Andropogon scoparius Michx., Little Bluestem.—Frequent.

Carex sprengellii Torr., Long-beaked Sedge.—Collected at Fargo in 1921, now perhaps destroyed.

Carex atherodes Spreng., Slough Sedge.—Frequent in wet places.

C. cristatella Britton, Crested Sedge.—Along river bank in 1933.

C. tetanica Schk., Wood's Sedge.—Collected in 1920.

C. torreyi Tuckerm., Torrey's Sedge.—Woods north of Moorhead in 1959.

C. saximontana Mack., Rocky Mountain Sedge.—Same as last, frequent.

Lemna perpusilla Torr., Minute Duckweed.—Collected by L. R. Waldron in 1908.

Cyperus acuminatus Torr. & Hook.—Frequent in low places.

C. schweinitzii Torr.—In sand ballast on railroad since 1942.

Eleocharis calva Torr.—Frequent in wet places.

Ulmus pumila L., Siberian Elm.—Natural seedling collected in 1954.

Parietaria pensylvanica Muhl., Pellitory.—Not collected until 1926 but presumably overlooked as it proves to be quite common here and elsewhere.

Juncus gerardi Loisel., Blackgrass.—Found in railroad ditch in 1954.

Zygadenus elegans Pursh, Camas.—A specimen by Lee in 1891 is labeled Fargo but I have not seen it in the present area.

Commandra pallida A.DC., Bastard Toadflax.—Perhaps overlooked before. It was collected in 1936 on railroad ballast and may have occurred in native prairie.

Polygonum amphibium L. —I find no confirmation of this but the variety *stipulaceum* (Coleman) Fern. is growing on railroad sand ballast. I have not found it in flower but it usually is cut down prior to blooming.

P. hydropiper L. Waterpepper. —Collected in 1939 and at Wild Rice (10 mi. south of Fargo) in 1924.

P. prolificum (Small) Robins.—This has been called *P. exsertum*. It is a slender plant that grows among grasses or on bare soil in low areas.

Rumex domesticus Hartm., House Dock. —Not recognized until 1955 when it was fairly common. The specimen previously reported as *R. occidentalis* is now placed here.

R. stenophyllus Ledeb.—First noted in 1955; frequent.

Chenopodium berlandieri Moq., Pit-seed Goosefoot.—This grows in broken places in grassland or along road and dry ditches, not so often in fields.

C. strictum Roth, Late Lambs Quarters.—This was not noted until about 1930 but one specimen identified by Wahl (1954) was collected in 1917. It has become very common, especially as a street and yard weed, also in fields since about 1945. Its flowering period (late August) is characteristic.

C. album, var. *stevensii* Aellen.—This variety was based on Fargo material. It seems rare but perhaps is common according to Wahl's interpretation.

C. bushianum Aellen., Bush's Goosefoot.—Frequent in wooded areas. Previously not distinguished from *C. album*. The forma *acutidentatum* (Aellen, 1929: 119) was based partly upon Fargo material.

Atriplex patula L.—The slender, typical form has become very aggressive in yards and gardens since 1921.

A. rosea L., Redscale.—This was found around streets in 1923 and invaded lawns to some extent, but seems to have disappeared.

A. glabriuscula Edmonston.—Well developed colonies of this were found in 1954 and 1955.

Cycloloma atriplicifolium (Spreng.) Coult., Tumbleweed.—Found in some abundance in the railroad yards at Dilworth, Minnesota, in 1958.

Kochia scoparia L., Burning Bush.—Has become exceedingly abundant and aggressive.

Salsola collina Pallas.—This seems the common form now. Determined by Aellen.

Amaranthus hybridus L.—A single plant was collected in 1921.

Mollugo verticillata L., Carpet Weed.—This persisted for a number of years about 1920-40, then apparently disappeared from the original location but was seen at another locality in 1953 and found at Jamestown, N.D., also along the railroad.

Agrostemma githago L., Corn Cockle.—Not seen in recent years.

Silene cserei Baum., Smooth Catchfly.—First collected in 1928 and is frequent in gravel ballast along railroads.

Cerastium vulgatum L., Mouse-ear Chickweed.—Appeared in many lawns about 1953 but seems not to persist.

Lychnis alba Mill., White Cockle.—Collected along railroad in 1922 but not found since.

Stellaria longipes Goldie.—The specimen by Bolley is now referred to *S. longifolia* Muhl.

Myosurus minimus L. Mousetail.—Collected at Fargo in 1930 but not seen since.

Alliaria officinalis Andr., Garlic Mustard.—On a vegetable farm near Moorhead in 1958, well established in edge of woods.

Cardaria draba (L.) Desv., Perennial Peppergrass.—Collected at Moorhead in 1921. Found at Fargo about 1930 and at several places in the county thereafter. The variety *repens* (Schrenk) Schultz appeared in the experiment station plots about 1935 but was eradicated.

C. pubescens (Meyer) Rollins.—This species was found in a brome grass plot in 1940 where it had been established for some time and still is present.

Lepidium ramosissimum A. Nels., Branched Peppergrass.—One or two plants have been found along streets and railroads. It has not persisted, although it is frequent in similar locations through central North Dakota.

L. perfoliatum L.—One plant was found in 1932 and several at Moorhead in 1958.

Brassica nigra (L.) Koch, Black Mustard.—Found in some quantity in 1955. Previously collected in 1901.

B. hirta Moench., White Mustard.—Found around a seed cleaning plant in 1942.

Camelina microcarpa Andr., Small-seeded False Flax.—Along railroad in 1955.

Arabis holboellii Hornem.—One plant was found along the railroad in 1947.

Berteroa incana (L.) DC., Hoary Cress.—Along railroad in 1946 and later.

Rorippa sylvestris (L.) Bess.—Collected in 1922 but station since destroyed.

Draba reptans (Lam.) Fern.—Several plants along railroad in 1947.

Sisymbrium officinale (L.) Scop., Hedge Mustard.—There is a specimen collected in 1902. Abundant in a sodded lawn in 1956 but not present the next year.

S. loeselii L.—A few plants were seen in 1956, a number in 1937 at Mapleton, 10 miles west and at Moorhead in 1948.

Descurainia sophia (L.) Webb., Flixweed.—This has become very abundant since 1920.

Hesperis matronalis L., Sweet Rocket.—A frequent escape from gardens.

Fragaria vesca, var. *americana* Porter.—Formerly frequent in aspen woods.

Potentilla anserina L., Silverweed.—A specimen was collected from a city lot in 1953. It was probably introduced there and was soon destroyed. The plant occurs in the Moorhead-Dilworth area but is not common.

Chamaerhodos nuttallii Pickering., Little Rose.—A colony along the railroad in 1947.

Prunus pumila L., Sand Cherry.—A plant brought in railroad ballast about 1940 is still thriving.

Astragalus striatus Nutt.—On ballast of railroad in 1942.

Oxytropis lambertii Pursh., Purple Loco.—On railroad in 1922.

Trifolium resupinatum L.—In lawn in 1941.

T. dubium Sibth.—Collected in new lawn in 1941.

Vicia americana, var. *angustifolia* Nees., Prairie Vetch.—Occasional along railroad.

Geranium pusillum L., Small Cranesbill.—In lawn in 1912.

Euphorbia marginata Pursh., Snow-on-the-mountain.—Frequently escapes from gardens but does not persist.

E. supina Raf. (*E. maculata* L.), Spotted Spurge.—Continues to grow along the railroad and was abundant at Dilworth in 1958.

E. maculata L. (*E. nutans* Lag.), Nodding Spurge.—One plant along railroad in 1929.

Polygala verticillata L., Whorled Milkwort.—Collected near Dilworth, Minn.

Impatiens capensis Meerb. (*I. biflora* Walt.), Spotted Touch-me-not.—This is the common form though *I. pallida* Nutt. has been found occasionally.

Rhamnus cathartica L., Common Buckthorn.—This has become widely established since about 1930.

Althaea officinalis L., Hollyhock.—Continues to volunteer freely.

Malva parviflora L., Small-flowered Mallow.—Common in a garden in 1958.

Elaeagnus angustifolia L., Russian Olive.—First noted as spread from plantings about 1950 and frequently thereafter.

Ammannia coccinea Rottb.—First noted at Fargo in 1923 and at nearby places later.

Epilobium angustifolium L., Fireweed.—Noted about 1920 in a wet spot along the railroad. The plant is only occasional and local in most of North Dakota.

Oenothera serrulata Nutt., Toothed-leaved Evening Primrose.—Collected in 1925. Its continued occurrence is dubious.

Lomatium orientale C. & R., Wild Parsley.—Collected along railroad in 1931.

- Anethum graveolens* L., Dill.—Commonly persists in gardens.
- Cornus stolonifera* Michx., Red Osier.—No specimen from the area is at hand but several from nearby.
- Lysimachia thrysifolia* L., Tufted Loosestrife.—Collected in low ground east of Moorhead.
- Apocynum medium* Greene.—Material collected in 1951 seems to be this form. It had not been recognized before.
- Asclepias speciosa* Torr., Showy Milkweed.—Frequent in low, saline soil.
- Cuscuta megalocarpa* Rydb., Large-fruited Dodder.—Material collected in 1950 seems referable to this form.
- Amsinckia retrorsa* Sucks., Buckthorn weed.—Collected along railroad in 1942 but soon destroyed.
- Hackelia virginiana* (L.) I. M. Johnston.—This was recognized in 1953 as abundant in one river bend and a specimen collected in 1934 is this species. It seemed not affected by a leaf spot which was abundant on *H. americana*.
- Verbena rigida* Spreng.—Plants were growing among trees on the Agricultural College campus in 1943 but did not persist.
- Glechoma hederacea* L., Ground Ivy.—Collected in Moorhead in 1921 and in Fargo in 1955.
- Galeopsis tetrahit* L., Hemp Nettle.—Along railroad in Moorhead in 1960.
- Molucella laevis* L., Shellflower.—Collected in Moorhead in 1959 where a house may have been removed (flood-control project).
- Hedeoma hispida* Pursh., Rough Pennyroyal.—Along railroad in 1925; in newly sodded lawn in 1959, few the next year.
- Salvia reflexa* Hornem., Lance-leaved Sage.—Collected in 1933 on roadside and in 1958 on river bank near Moorhead.
- Solanum dulcamara* L., Bittersweet.—In dooryard at Fargo, not known to have been planted.
- Physalis heterophylla* Nees.—Along railroad, 1921 and later.
- Penstemon albidus* Nutt., White Beardtongue.—Along railroad in 1925.
- Plantago eriopoda* Torr., Alkali Plantain.—Collected at Moorhead in 1921.
- P. indica* L.—Along railroad at Dilworth in 1958.
- Galium trifidum* L., Small Bedstraw.—Collected north of Moorhead in 1955.
- Lonicera tatarica* L., Tartarian Honeysuckle.—Volunteers freely from plantings.
- Sambucus canadensis* L., Black-berried Elder.—Collected in Moorhead in 1959, probably escaped from plantings.
- Campanula rapunculoides* L., Creeping Bellflower.—This is often planted and has spread into lawns in recent years.
- C. rotundifolia* L., Blue Bell.—Along railroad in 1925.
- Liatris punctata* Hook., Narrow-leaved Blazing Star.—Along railroad in 1920.
- L. pycnostachya* Michx., Tall Blazing Star.—This occurs in low prairie along the railroad at Dilworth.
- Chrysopsis villosa* Pursh., Golden Aster.—Frequent along railroad since 1917.
- Solidago flexicaulis* L., Broad-leaved Goldenrod.—This still grows where it was found in 1915, the area now in the Edgewood Golf Course.
- Aster sericeus* Vent., Silky Aster.—Along railroad in 1920; common at Muskoda, 15 miles east.
- Antennaria microphylla* Rydb.—A specimen labeled "Fargo, Field in 1891" has been verified by Cronquist but the plant has not been seen recently.

Helianthus nuttallii T. & G., Nuttall's Sunflower.—A Fargo specimen was determined as this by E. E. Watson.

Coreopsis tinctoria L., Tickseed.—Some plants persisted for many years along the edge of a field near Fargo.

Bellis perennis L., English Daisy.—A few plants in flower were found in a lawn in 1955.

Echinacea angustifolia DC, Purple Coneflower.—Along railroad in 1923.

Galinsoga ciliata (Raf). Blake., Quickweed.—This has appeared in several places since 1937 and seems now established.

G. parviflora Cav.—Found in flowerpot in 1929 and in door yards in both Fargo and Moorhead in 1958.

Matricaria maritima L., Scentless Chamomile.—Two plants by railroad in 1958.

Arctium tomentosum Mill.—A colony, apparently two or three years old, was found in 1956.

Carduus acanthoides L., Welled Thistle.—One plant was found in 1940, a large colony at another place in 1947 and some at another location in 1956.

Artemisia glauca Pall., Green Sage.—Along railroad in 1942 and later.

Centaurea repens L., Russian Knapweed.—A colony in a brome grass pasture on the college grounds was first noticed in 1937.

C. maculosa Lam., Spotted Knapweed.—A few plants were found along the railroad in 1956 but were destroyed the next year. It had been established in a farmyard about 20 miles east for many years.

Lygodesmia juncea (Pursh) D. Don., Skeleton Weed.—Along railroad in 1934.

Tragopogon major Jacq., Goatsbeard.—This is the only form found here.

Taraxacum koksagyz Robin., Russian Dandelion.—A few plants where seed had been cleaned in 1942 but none had been found near the field where plants were grown. They are well established near our building; begin flowering at the same time as *T. officinale*, but flower heads remain open until late afternoon.

Crepis tectorum L., Hawk's-beard.—Along railroad in Moorhead in 1958.

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Some Ecological Characteristics of the Molluscan Fauna of a Typical Grassland Situation in East Central Kansas¹

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ABSTRACT: A survey of some of the ecological associations of the molluscan fauna found in a typical grassland situation was conducted on the Ross Natural History Reservation, Lyon and Chase counties, Kansas, during the summer of 1960. The collecting stations were selected for their differences in habitat conditions, and soil or water analyses were conducted at each. Associated vegetation was studied in detail.

Six species of aquatic mollusks and 16 species of terrestrial snails were collected. *Physa hawnii* was the most common aquatic snail found, and *Gastrocopta armifera* the most abundant terrestrial species. Two pelecypods, *Unio merus tetralasmus* and one *Sphaerium*, were found. Many specimens of *Pupoides albilabris*, *Gastrocopta procer*a, *Zonitoides arboreus*, *Vallonia parvula*, and *Succinea* sp. were collected. Less abundant species, usually found in moist environments included *Gastrocopta contracta*, *G. tappaniana*, *Helicodiscus parallelus*, *Retinella indentata*, *Hawaia minuscula*, and *Stenotrema lei aliciae*.

INTRODUCTION

The object of this report is to record some of the ecological associations of the molluscan fauna found in a typical grassland situation. The study area included several different habitats on the Ross Natural History Reservation of Kansas State Teachers College, Emporia.

The reservation is located on the eastern edge of the Flint Hills Upland of east central Kansas. This area of rolling prairie hills crosses the state of Kansas and extends into Nebraska to the north, and southwards into Oklahoma. The hills serve as a sort of ecological barrier, and many species do not extend further west into the drier portions of the state. Since the reservation is in an area that was once cultivated and covered with orchards, and is still grazed, the information included in this study should be useful in determining the changes in molluscan populations as the reservation reverts to a natural condition.

HISTORICAL REVIEW OF STUDIES ON KANSAS MOLLUSKS

The Mollusca of Kansas received little attention until the early 1940's, although the earliest studies began over 75 years ago. In 1884, F. W. Cragin began a series of surveys of the flora and fauna of the state, sponsored by Washburn College in Topeka. Cragin was

¹ This study was supported by grant NSF G-11470 of the National Science Foundation to Kansas State Teachers College, Emporia.

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also editor of the *Bulletin of Washburn Laboratory of Natural History*. In this bulletin, R. Ellsworth Call published a series of papers on the molluscan fauna of Kansas, and Binney and Gray (1885) listed land shells of northeast Kansas.

Hanna (1909) mentioned 75 species and subspecies of gastropods in Douglas County and in the drift along the Kansas River. Franzen and Leonard (1942) conducted a preliminary survey of Kingman County, Kansas, and collected 26 species and subspecies of gastropods. Franzen and Leonard (1943) reported 16 freshwater mussels and 31 species and subspecies of gastropods from a series of 11 collecting stations in the Wakarusa River valley, a small tributary of the Kansas River. The same year, Alice E. Leonard (1943) reported five species of pelecypods and 21 species and subspecies of gastropods from Meade and Clark Counties, Kansas, most of them from the ungrazed spring areas in Meade County State Park. Franzen (1944) discussed 12 new species and subspecies of gastropods from the eastern two tiers of counties in Kansas. Leonard and Leonard (1946) reported 16 species of unionid mussels, 6 species of aquatic gastropods, and 19 species and subspecies of gastropods from eight collecting stations in Greenwood County, southwestern Kansas. The following year, Franzen (1947) listed the living and fossil Pupillidae of the Sanborn area in northwest Kansas. Franzen and Leonard (1947) reviewed 33 species of living and fossil Pupillidae known in Kansas.

Leonard and Goble (1952) collected 4 species of aquatic mollusca and 21 species of terrestrial gastropods at ten stations selected for their differences in local habitat conditions at the University of Kansas Natural History Reservation. Fitch and Lokke (1956) studied past conditions on the University of Kansas Natural History Reservation as indicated by the durable molluscan shells which persist in the soil long after plant associations and physical features of the environment have changed. Miles (1958) reviewed the three genera and seven species of succineids in Kansas as identified by their soft parts, especially their genitalia, since the shells of some of the succineids are of little taxonomic use. One of the most complete publications on mollusca of Kansas is the *Handbook of Gastropods in Kansas* by Leonard (1959).

HISTORY AND DESCRIPTION OF THE AREA

The 1040-acre Ross Natural History Reservation is located approximately 4 miles west of Americus or 14 miles northwest of Emporia. The reservation, as described by Hartman (1960), is primarily undulating to rolling bluestem grass prairie. The upland terrain is broken by several shallow ridges and limestone outcrops. A small seasonal creek and several other drainages cross the area. The total Lyon County area is 960 acres and includes portions of sections 7, 8, and 18 in T18S, R9E, section 12 (Hartman, 1960). The remainder of the reservation is in Chase County.

The reservation is located on the east of the Flint Hills Upland and lies in an area once known as Fruitland because of the extensive orchards planted by settlers in the late 1880's. Heavy droughts and recurrent invasions of grasshoppers and chinch bugs discouraged farming and the area is returning to grassland. None of the reservation is under cultivation at the present time. Hartman (1960) records the soils on the reservation as being medium to dark grayish-brown, stony, silty clay loams. Their geologic parent materials are limestone, cherty limestone, calcareous shales, and loess, with most of the soils adapted to native pastures.

The reservation is grazed at present and Hartman reports that there are probably no prairie areas on the reservation that have not been grazed in the last 10 years, although the extent of grazing has varied considerably. The dominant flora of the unbroken upland prairie is little bluestem (*Andropogon scoparius*) and Indian grass (*Sorghastrum nutans*), while the scattered, moderately grazed areas have a thinner cover of little bluestem, side-oats grama (*Bouteloua curtipendula*) and tall dropseed (*Sporobolus asper*).

The major wooded habitats on the reservation include a ravine beginning in Chase County and extending across the county line. A somewhat smaller wooded area lies along the ravine in section A on the eastern edge of the reservation. Several hedgerows are located on the reservation, the most extensive being found along the abandoned roadway of A58, as shown on Figure 1.

The major aquatic habitats include three ponds, the largest of which is Gladfelter Pond in B48. Smaller ponds are located in A5

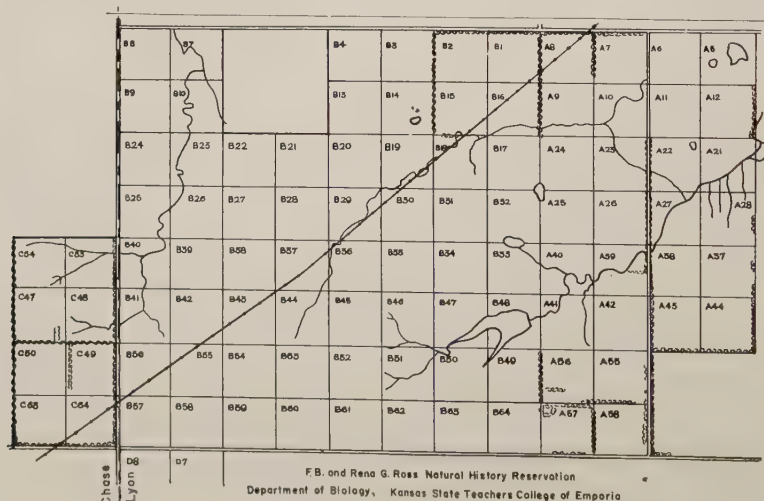


Fig. 1.—Map of the Ross Natural History Reservation, Lyon and Chase counties, Kansas. Each numbered square represents an area of ten acres.

and D10. The reservation is drained by three small streams. One of the streams originates in the wooded ravine in Chase County and flows east, then north. The second flows on the east slope of the upland prairie and flows northeast. The third consists of the watershed for Gladfelter Pond and flows northeast along a winding and wooded course.

Other habitats include several abandoned homesteads, an abandoned limestone quarry in B26, a small spring in A39 and several rocky prairie slopes and prairie washes.

Since acquiring the reservation in 1958, the Biology Department has planted a one-acre feed patch for wildlife in A56, a windbreak and several small groups of evergreens around the headquarters area in A56 and around Gladfelter Pond in B48. Several natural enclosures and lean-to shelters have been constructed and multiflora roses have been planted in different areas to provide protection for wildlife.

CLIMATE

The mean annual rainfall of the county is 34.10 inches; the monthly precipitation varies from an average of 0.81 inches in January to 5.20 inches in May. About 70 per cent of the annual precipitation is received between April 1 and September 30 and the monthly average for this period is 4.04 inches. The total amount of rainfall during the driest year (1936) was 18.13 inches and for the wettest year (1941) 53.37 inches.

The mean annual temperature for the year is 55.8°F, with the monthly average varying from 30.7°F in January to 79.5°F in July. The average temperature from April 1 to September 30 is 68.8°F. The average date of the last killing frost is April 1 and for the first killing frost, October 18. The growing season averages 187 days.

The average relative humidity in Kansas is lower than in states of the east and southeast. The low relative humidity favors rapid evaporation. In the eastern third of the state relative humidity is higher than the rest of the state and ranges from 45 to 50 per cent at mid-day in July to 70 per cent in winter at the same time of day. Most of the year, the prevailing winds are from the south resulting in a drying effect on the soil of the south facing slopes. Most of the above climatological data were abstracted from Flora (1948).

METHODS

Field methods.—A general survey of the reservation was conducted the second week in June, 1960, to select the collecting stations. Following this, collection trips were made on alternate days from June 15 to August 4, 1960. A field sheet kept for each station included a list of dominant flora, a general area description, and a field number for future reference. Shells were placed in small vials for transport to the laboratory. Jewelers' forceps were useful for collecting smaller species. A set of soil sieves was used for recovering specimens from loose soil, gravel, and debris.

Laboratory methods.—The snails were killed and the shells cleaned by immersing them in boiling, soapy water. Removal of the soft bodies of larger specimens proved advisable before they were examined under a binocular microscope.

References used for identification included Pilsbry (1939, 1940, 1946, and 1948), Baker (1928, 1939) and Leonard (1959). Questionable determinations were verified by Mr. Tong-Yun Ho and Mr. Harold Murray of the University of Kansas. The identified specimens were assigned a catalogue number in the mollusk collection of the Kansas State Teachers College, Emporia.

Water analysis.—Water samples were taken at each aquatic station and were checked for dissolved oxygen, carbon dioxide, phenolphthalein and methyl orange alkalinity, total hardness, seston, turbidity, and pH. The test for dissolved oxygen by the Winkler method and tests for carbon dioxide, phenolphthalein and methyl orange alkalinity, and total hardness by the soap method are described by Theroux, Eldridge and Mallman (1943). Seston determination is described by Chandler (1942), and the determination of turbidity with a U.S. Geological Survey turbidimeter, by Welch (1948). The pH was determined with a Beckman zeromatic pH meter.

Soil analysis.—A soil sample was taken at each terrestrial station and was transported to the laboratory in small jars. The sample was then air dried and sifted through a U.S. standard soil sieve with 1.19 mm mesh. Samples were tested for available phosphorus, potassium, and nitrogen, organic matter and pH. All tests were made using LaMotte soil analysis kits as described in the LaMotte Soil Handbook (1956).

COLLECTION AREAS

AQUATIC HABITATS

Three ponds and one stream were surveyed on the reservation. The stream, studied June 23, passes from Gladfelter Pond in B48 and proceeds northeast until it leaves the reservation in A21 (Fig. 1). It is joined by several other small streams in A40, A39 and A27. About one-half of the length is shaded or partially shaded and part is bordered by tall grasses. Except for periods following rains, the width varies from about one to five feet, the depth ranges from several inches to several feet and for the most part the bank is abrupt and bare. Much of the creek bed is over a limestone outcrop and there are many limestone rocks on the creek bottom. Most of the specimens were collected on and under rocks, on vegetation, and on submerged branches. The hardness and methyl orange alkalinity were comparatively high (Table I). Living snails were represented by the largest colony of *Physa hawnii* on the reservation and a few *Lymnaea bulimoides techella* (Table III). Nine *Succinea* sp. were collected at this station and several terrestrial shells were sifted from the bottom mud. *Physa hawnii* was also common in the stream surveyed on the University of Kansas Reservation (Leonard and Goble, 1952).

Three ponds were surveyed on the reservation on July 22. Glad-

felter Pond, located in B48 (Fig. 1), was constructed in June, 1958, and is used by cattle. Almost all of the moluscan specimens were taken from a neck in the southwest corner of the pond. The water was receding and many dead shells were picked up on the drying ground around the edge in this neck. Many living snails as well as a few shells of terrestrial forms were sifted from the bottom silt. *Physa hawnii* was abundant and only 16 *Lymnaea bulimoides techella* were collected (Table III). *Succinea* sp. was fairly abundant at this station.

Two unshaded, mud-bottom pools were surveyed in A5; the larger was about 60 feet in diameter and the smaller about half that, although both were gradually receding. Both ponds serve as a source of water for cattle and were turbid. Limestone rocks were fairly abundant around the edge in the smaller pond and less numerous in the other. The smaller body of water represented the most alkaline condition on the reservation (pH 8.7), the highest temperature (98°F), the highest oxygen content (12.0 ppm), the lowest methyl orange alkalinity (128 ppm), the highest phenolphthalein alkalinity (4 ppm), the softest water (108 ppm), and the lowest per cent of organic material (24.4%) in the seston. The analysis revealed no free carbon dioxide (Table I). Similar results were obtained from the water analysis of the larger pond. *Physa hawnii* was the most abundant snail at this station (Table III). In the smaller body of water *Helisoma trivolvis* and *Sphaerium* sp. were fairly abundant. At the larger pond, two *Bulimulus dealbatus* were found on the dam and several shells of *Uniomorus tetralasmus* were found at the edge. Thus, this station yielded four species not collected elsewhere on the reservation. Leonard and Goble (1952) found *Helisoma trivolvis*, *Physa hawnii*, *Sphaerium* sp. and *Succinea concordiales* in a silted pond at the Kansas University Natural History Reservation.

TABLE I.—Water data at the five aquatic stations on the reservation

	Spring A39	Pond B48	L. Pond A5	S. Pond A5	Stream B48-A21
Water					
Temperature (°F)	59	83	97	98	81
pH	7.2	8.2	8.4	8.7	8.2
Dissolved					
Oxygen (ppm)	5.8	4.6	5.6	12.0	6.8
Free Carbon					
Dioxide (ppm)	19.0	0.2	0.0	0.0	2.0
Phenolphthalein alkalinity (ppm)	0.0	0.0	2.0	4.0	0.0
Methyl orange alkalinity (ppm)	315.	165.	135.	128.	265.
Hardness (ppm)	216.	132.	112.	108.	192.
Organic Matter (%)	36.4	27.0	30.7	24.4	27.1
Turbidity (ppm)	----	60.	250.	150.	----

SPRING AREA

The spring area, located in the southeast corner of A39, was surveyed on June 15. This habitat consists of an unshaded body of water about 3 feet wide, 10 feet long, and several inches deep, matted with watercress (*Nasturtium officinale*) and bordered at the head and on the sides with limestone rocks. The water seeps down a gradual northeast-facing slope forming a marshy environment with an abundance of great bulrush (*Scirpus validus*). Clumps of Indian grass and big bluestem (*Andropogon gerardi*) surround the limestone rocks.

An analysis of the spring water revealed that the water contained the highest free carbon dioxide content (19.0 ppm), the highest methyl orange alkalinity (315 ppm), the greatest hardness (216 ppm), the lowest pH (7.2), and the lowest temperature (59°F) (Table I). The results obtained from the water analysis at this station were in direct contrast to those obtained from the small pond in A5. In the soil surrounding the spring the pH and the nitrogen content were higher than at any other area surveyed (Table II). Organic matter was comparatively high. Burch (1955) found a close correlation between organic matter and the distribution of snails.

Twelve species of mollusks were taken from the spring area (Table III), mostly from the moist soil under the limestone rocks. The three most abundant species were in order: *Gastrocopta armifera*, *Succinea* sp., and *Vallonia parvula*, and these comprised about 70 per cent of the collection. Over 16 per cent of the specimens were *Pupoides albilabris* and *Retinella indentata*. Thus, the remaining seven species

TABLE II.—Soil data from the 16 terrestrial stations on the reservation

Station	pH	N (lbs/- acre)	P (lbs/- acre)	K (lbs/- acre)	Or- ganic (%)
Spring (A39)	7.6	32	200+	120	5.18
Decaying log (C33)	7.4	8	150	185	3.01
Wooded area (A21)	7.4	8	200+	155	4.72
Wooded area (C33)	7.4	24	150	110	1.92
Hedgerow (A42-A39)	7.2	3	200+	140	5.31
Hedgerow (B1-B16)	7.4	8	200+	275	3.45
Abandoned farmsite (C63)	6.8	8	200+	275	4.92
Prairie wash (B4)	7.4	3	200+	90	2.98
Limestone quarry (B39)	7.4	3	200+	135	2.09
South facing slope (D7)	7.4	8	200+	160	6.03
West facing slope (B26)	6.0	8	200+	125	5.38
Limestone ledge (C33)	7.4	3	200+	90	6.62
Prairie area (A6)	6.0	3	150	140	4.49
Prairie area (B35)	6.2	24	200+	160	4.69
Prairie area (B53)	6.6	3	200+	150	4.72
Prairie area (B8)	6.2	3	150	120	3.90

comprised only 14 per cent of the collection. Ten of the 11 *Lymnaea parva* taken during the study were collected at this habitat and this was one of two stations in which *Gastrocopta tappaniana* was collected. This was the most prolific station for *Hawaiiia minuscula*. The nearby area produced a few *Succinea* sp. and no snails were found among the matted watercress roots.

DECAYING LOG

A decaying log located in the heavily wooded area of C33 was studied on July 15. The log was about one foot in diameter and two and one-half feet long, and was easily broken into small pieces for study. The soil underneath the log was rich and moist. Only three species were collected at this station and only *Zonitoides arboreus* was found in abundance. This species was also abundant in a decaying log surveyed on the Kansas University Natural History Reservation (Leonard and Goble, 1952).

WOODED AREAS

Two wooded areas were surveyed on the reservation. The wooded habitat along the stream in the south part of A21 was surveyed on June 17. On the gentle slopes, clumps and scattered trees of cottonwood (*Populus deltoides*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), osage orange (*Maclura pomifera*), and black walnut (*Juglans nigra*) occur in the area. Several thickets of fragrant sumac (*Rhus aromatica*) and dogwood (*Cornus drumindii*) were noted near the creek. The floor of this wooded area is shaded and moist. Rotting logs and moist humus on loose rich soil served as profitable collecting areas.

On July '28, a survey was made on the most heavily wooded area on the reservation, in C33. The largest trees in this area are hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), red elm (*Ulmus rubra*), black walnut and osage orange. Thickets of fragrant sumac, coralberry (*Symphoricarpos orbiculatus*), and dogwood are found on the slopes. Also patches of gooseberry (*Ribes missouriense*), gaura (*Gaura parviflora*), poison ivy (*Rhus radicans*) and ironweed (*Vernonia baldwini*) inhabit the floor of this area. Some of these plants came in from the nearby prairie area. The undercover is heavily trampled by cattle. There are a few small limestone rocks and many large logs and brush piles which served as excellent collection sites. No unusual soil conditions were noted at either of the wooded habitats, except that the organic matter in C33 was low (Table II).

Thirteen species were collected in A21 and only eight in C33 (Table III). However, the latter collection was made during drier conditions. The A21 wooded area yielded more species than any other collecting station. *Gastrocopta armifera* was the dominant mollusk of both wooded areas, comprising about 40 per cent of the collection in each. *Vallonia parvula* and *Zonitoides arboreus* comprised over 36 per cent of the A21 collection. Thus, the remaining ten species com-

prised only 23 per cent of the collection. The A21 area was the most profitable area on the reservation for *Gastrocopta contracta* and this station was one of two in which *Gastrocopta tappaniana* was collected. Seven species were represented in the A21 wooded area which were absent in the other habitats. However, *Stenotrema leai aliciae* was collected only in C33. About two-thirds of the collection in C33 represented *Gastrocopta armifera* and *Zonitoides arboreus*. *Vallonia parvula*, very common in A21, was not as abundant in C33 and *Succinea* sp. was twice as abundant in C33.

HEDGEROWS

Two hedgerows were surveyed on the reservation. One, located on the east border of A39 and A42, was surveyed July 20. The dominant tree is osage orange and interspersed are honey locust (*Gleditsia triacanthos*), American elm, and hackberry with some thickets of dogwood and sumac nearby. The ground slopes and is heavily shaded and contains loose, wet soil, sparse vegetation, a few limestone rocks, and has abundant leaf litter and twigs. The hedge contains a high percentage of organic matter in the soil compared to the other areas (Table II).

The second hedge, located on the east border of B1 and B16, was studied August 2, and contains osage orange with scattered honey locust and American elm. Most species were collected in the heavy litter and leaves on the loose, moist soil. Very little ground vegetation exists. The potassium content was relatively high at this station (Table II). Burch (1955) stated that potassium may have some indirect effect, but is not assumed to be a limiting factor.

Ten species were taken from the A42-A39 hedgerow, which was the richer of the two hedges in terms of species and individuals (Table III). *Gastrocopta armifera* comprised over 34 per cent of the collection and *Vallonia parvula* over 24 per cent. *Retinella indentata*, *Zonitoides arboreus* and *Stenotrema leai aliciae* were fairly abundant at A42-39, but were not taken from the other hedgerow. Although seven species were collected at the B1-16 hedgerow, only *Vallonia parvula* and *Gastrocopta armifera* were abundant making up 88 per cent of the collection. *Succinea* sp. was fairly abundant at the B1-16 hedge and only one was collected at the other hedge. The more prolific hedge also contained the only *Gastrocopta pentodon* collected on the reservation.

ABANDONED HOMESTEAD

One abandoned homestead in C63 was surveyed on August 4. The limestone shell of a farmhouse still stands and many limestone rocks are located around the house. Because of the artificial situation, there is a wide variety of plants in the area. Apparently, winter and spring precipitation accumulates in the dirt cellar. A high potassium content was measured in the soil sample taken from the cellar floor (Table II). Nineteen shells of *Physa hawnii* were collected on the

moist floor (Table III). Nine *Gastrocopta armifera* were found around the farmhouse.

LIMESTONE OUTCROPS

Five limestone outcrops were surveyed. Van Cleave (1953) states that mollusks are intimately dependent upon a lime supply for the production of their shells and the correlation is so close that collectors of shells have long realized that limestone outcrops and streams flowing through limestone are favorable collecting areas. Burch (1955) reports that calcium appears to be one of the primary materials in the soil which limit the distribution of land snails.

The first area, surveyed June 27, is a northwest-facing, unshaded prairie wash located in B4. This wash contains medium to large limestone rocks on a gradual slope. Prairie grasses surround the rocks, and numerous snails were found among the roots which were exposed when the rocks were overturned. The soil under the rocks was moist and the wash drains into a roadside ditch. The potassium content was low at this station (Table II). This limestone habitat yielded only three species in any abundance. The 639 *Gastrocopta armifera* represented the largest number of individuals of one species taken at one station. *Pupoides albilabris* was more abundant here than at any other station and *Gastrocopta procera* was also common.

A second limestone outcrop is an abandoned rock quarry on a ridge in B39, which was surveyed June 29. A depression in the area about 50 feet in diameter is surrounded by very large limestone rocks. Winter and early spring precipitation accumulates in the depression (Hartman, 1960); however, on the date of the survey the soil was very dry. There was evidence of heavy trampling by cattle in the depression, and vegetation is very scanty. Towards the periphery and outside of the depression there are clumps of big bluestem, switchgrass (*Panicum virgatum*), barnyard grass (*Echinochloa crusgalli*), and wild rye (*Elymus canadensis*). The percentage of organic matter was low at this area (Table II). No living snails were found in the quarry. However, 209 shells of *Lymnaea bulimoides techella* were found mainly under the smaller limestone rocks. No other species were found in the depression area; however, a few others were taken from under the small rocks surrounding the quarry.

The third limestone outcrop, surveyed July 6, is a south-facing, unshaded habitat in D7 (Fig. 1). There were many small to medium sized limestone rocks and the soil underneath was very dry. The ground was trampled and the area heavily grazed. The grasses were cut off at the roots and could not be identified. Some of the common plants in the area were leadplant (*Amorpha canescens*), ironweed, silverleaf scurfpea (*Psoralea agrophylla*), black sampson (*Echinacea pallida*), and thistle (*Cirsium altissimum*). The organic matter was high compared to the other areas (Table II). Only three species were collected here: *Pupoides albilabris*, *Gastrocopta armifera*, and *G. procera* (Table II). All were fairly abundant and represented only by dead shells.

The fourth limestone area is a heavily shaded ledge in a wooded area along both sides of a stream in C33. This region was surveyed July 15. There is a fairly sharp slope from the ledge to the creek and smaller limestone rocks are found on this slope. The ledge runs east and west, and it was noted that there were many more snails on the north-facing ledge. Some of the dominant vegetation in the area is black locust (*Robinia pseudoacacia*), honey locust, osage orange, smooth and fragrant sumac, dogwood, hackberry, American Elm, green ash, and black walnut. The ground cover is not lush. Several large limestone rocks in the ledges were overturned and the soil appeared to be rich and moist. The highest percentage of organic matter on the reservation was measured at this station. Over 56 per cent of the specimens collected were *Vallonia parvula* or *Gastrocopta armifera*. The largest population on the reservation of *V. parvula*, *Helicodiscus parallelus* and *Stenotrema leai aliciae* was taken at this station.

The last limestone outcrop, surveyed August 2, is in B26. The largest rocks on this west-facing slope were moist underneath and most of the shells were collected there. The dominant vegetation is little bluestem, side oats grama, silverleaf scurfpea, wild indigo (*Baptisia leucuphea*), ironweed, leadplant, and patches of fragrant sumac. The lowest pH on the reservation was measured at this station and the organic content was high. Over 65 per cent of the specimens taken were *Gastrocopta armifera*. The largest population of *Gastrocopta procera* was taken at this station. The only other species taken in large numbers was *Pupoides albilabris*.

In general, *G. Armifera* was the most common snail in the unshaded limestone outcrops. *Pupoides albilabris* and *G. procera* were also well represented. The unique quarry presented a different situation. *Vallonia parvula* was prevalent in the shaded limestone outcrop.

PRAIRIE AREAS

Collections were made from four grazed, open prairie areas on the reservation. The areas surveyed were in A6, B35, B53, and B8. Hartman (1960) reports that little bluestem and Indian grass dominate the unbroken upland in the western two-thirds of the B section and the northern half of section D. The scattered, moderately grazed areas have a thinner cover of little bluestem, side-oats grama and tall dropseed (*Sporobolus asper*). Denuded areas, ravines and broad washes were invaded by arrow-feather (*Aristida purpurascens*), goosegrass (*Eleusine indica*), Virginia wild rye (*Elymus virginicus*), muhly (*Muhlenbergia brachyphylla*), witch grass (*Panicum capillare*) and yellow bristle grass (*Setaria lutescens*). Some of the more frequently occurring prairie vegetation noted during the summer were leadplant, ironweed, silverleaf scurfpea, thistle, common ragweed (*Ambrosia artemisiifolia*), milkweed, yarrow (*Achillea millefolium*), daisy fleabane (*Erigeron ramosus*) and broomweed (*Gutierrezia dracunculoides*). Most of the gastropods taken from the prairie areas were represented only by shells.

The A6 prairie area, surveyed June 21, has a thick cover of prairie vegetation. The area is flat and is in a region where the surface soil is described as moderately deep, dark, friable and silt to clay (Eikleberry, Fly, and Dodge, 1956). The pH at this station was 6.0, one of the most acid conditions on the reservation (Table II). Most of the specimens taken at this station were collected under cow dung. Limestone rocks were very scarce. Five species were taken at this station. *Gastrocopta armifera* was common and comprised over 78 per cent of the collection. *Pupoides albilabris*, *Gastrocopta procera*, and *Helicodiscus parallelus* were sparsely represented at this station.

The B35 area, surveyed July 1, is on a gradual, northwest-facing slope next to the crest of a hill. It was described as being in the same soil region as A6 (Eikleberry, Fly, and Dodge, 1956). A few limestone rocks are present and a thicket of smooth sumac is on the north end of the collection area. The soil pH was 6.2 and the nitrogen content was high compared to that of the other stations. *Gastrocopta procera*, *Pupoides albilabris*, and *Helicodiscus parallelus* were sparsely represented at this station.

Prairie area B53, surveyed July 13, is on a gradual, south-facing slope. Limestone rocks and dung piles are scarce at this station. This area has a fairly thick cover of prairie vegetation. Only 21 specimens were taken from this area.

Area B8, surveyed August 4, has more limestone rocks and dung piles than any other prairie area. The surface soils are light brown and are three to five inches deep with gravel or chert subsoils (Eikleberry, Fly, and Dodge, 1956). The soil is acid in this prairie area (Table II). Only three species were collected. *Gastrocopta armifera* comprised almost 83 per cent of the collection. *Pupoides albilabris* and *Gastrocopta procera* were the other two species collected.

The soil pH at the prairie areas was acid. Burch (1955) stated that pH has little influence and is not a limiting factor in the distribution of snails. In general, *G. armifera*, *G. procera*, and *P. albilabris* were the most abundant snails in the prairie. In the grazed meadow on the University of Kansas Reservation, Leonard and Goble (1952) found only *G. armifera*, *G. procera*, and *Bulimulus dealbatus*, and all of these were rare.

ACCOUNTS OF SPECIES

Physa hawnii Lea

This midwestern species is found in the eastern third of Kansas with scattered records farther west. *P. hawnii*, a typical pond snail, is one of the most common aquatic gastropods in Kansas, and is found in roadside ditches, streams, lakes, and rivers. Most of the specimens were found on rocks and dead sticks just under the surface of the water in the ponds (B48, A5) and the stream (B48, A21), while a few were taken from the stems of aquatic plants. Although very common at the aquatic stations on the reservation, a few shells were

TABLE III.—Distribution of molluscan species according to habitat on the Ross Natural History Reservation (the numbers represent the number of each species collected at each area)

[illegible]

taken from the clay basement of an abandoned homestead in C63 which probably contained water during much of the year.

Fifty individuals from the stream were checked for trematode parasites. One was found to be infected with a fluke of the Xiphidiorcercaria group.

Helisoma trivolvis lentum (Say)

This species, common throughout Kansas and much of eastern North America, inhabits rivers, small streams, lakes, ponds, and roadside ditches. Large colonies are often found in quiet, more or less stagnant, shallow water on ooze-covered bottoms and on rocks and dead plants. Alice Leonard (1943) finds that it can survive long periods of drought, apparently by burrowing into the mud at the bottoms of drying pools.

Helisoma trivolvis lentum was found at one station on the reservation, the smaller of the two ponds in A5. Forty-four specimens, most of them living, were taken from the rocks, sticks, and mud bottom of the pond.

Lymnaea parva Lea

Widely distributed east of the Rockies, this snail is found primarily in the eastern half in Kansas. It is rarely found in water although it does require a rather moist habitat, often living on sticks, stones, or mud flats on exposed mud bottoms of transient pools and on moist drift along stream banks.

Lymnaea parva was not common on the reservation and was collected at only two stations, the spring (A39) and the wooded area (A21). Dead shells were found under limestone rocks around the spring and under small logs in the wooded area.

Lymnaea bulimoides techella (Haldeman)

In contrast to the three species just discussed, this is primarily a southwestern form, extending into northern Mexico (Baker, 1911). The study area is near the northeastern limit of distribution of this species, and in this case represents an area of overlap between elements characteristic of southern and northern faunas.

Lymnaea bulimoides techella often may be found in ephemeral pools where it appears in large numbers for a few weeks in early spring. Few adults are seen through the hot summer months (Franzen and Leonard, 1943). It commonly lives in shallow water with a mud or ooze-covered bottom. In Franklin County, Kansas, it was found living in a large rock quarry at the edges of several shallow pools, by Leonard (1955).

Many dead shells were collected from a depression in the abandoned quarry (B26) on the reservation. The depression was dry at the time of the collection, but it usually contains a small pool of water. Living specimens were taken from rocks and plants on the edges of the ponds (B48, A5) and dead shells were recovered by screening mud and gravel from the bottom of the ponds and the

stream (B48-A21). Although this species was collected at six stations, the quarry (B26) was the only one containing great numbers of shells.

Gastrocopta armifera (Say)

Leonard and Goble (1952) list this wide-ranging species as common throughout Kansas. Although Baker (1939) notes that this is a characteristic snail of prairie regions, preferring dry habitats, we found that it was most abundant in moister areas where there were many limestone rocks. Franzen and Leonard (1947) state that in prolonged dry, hot summer months *G. armifera* is able to aestivate, making possible its survival in Kansas. However, two of the three collections in which this species did not occur were from open prairie areas (B35, B53), indicating that conditions there may be too severe even for this tolerant form. Archer (1937) finds *G. armifera* to be rare or absent in woods, but our study indicates that the species may be found there, confirming the observations of Alice Leonard (1943).

This is the most common snail on the reservation; it was collected at 13 of 16 terrestrial stations. It was extremely abundant in the dry bed of a prairie wash gully in section B4, where 639 specimens were taken, 261 of which were under a single rock. Many specimens were also found in rotten log and leaf litter in wooded areas, and a few were turned up under cow dung.

Gastrocopta contracta (Say)

In Kansas, *G. contracta* is found primarily in the eastern half of the state; it is also recorded from Canada, Mexico, and many areas in the United States. This snail occupies almost as wide a variety of habitats as *Gastrocopta armifera*, but does not seem to be as abundant at any given locality. Its usual habitat is on shaded slopes along water-courses under dead wood, leaf mold, and grass (Franzen and Leonard, 1947). It exhibits a well defined preference for mesic habitats, but also occurs in relatively dry places (Fitch and Lokke, 1956).

In their survey, Leonard and Goble (1952) found *G. contracta* at six of eight terrestrial stations, but nowhere was it abundant.

Gastrocopta contracta was collected in relatively small numbers at 5 of 16 terrestrial stations on the Ross Reservation. Specimens were taken from a west-facing slope (B26), limestone ledge (C33), spring area (A39), and wooded slope (A21). Most of the shells occurred under rocks in fairly moist conditions or under leaf mold in shaded areas. A few dead shells were recovered from screenings of debris from the limestone ledge.

Gastrocopta pentodon (Say)

This species occurs in wooded areas and under suitable cover in grasslands (Leonard, 1959). Baker (1939) states that it is seldom found in wet places. In Kansas, it is found in the southeastern portion; the range of the species in America is from Canada southward to Guatemala.

Two dead shells found in leaf litter in a hedgerow (A42-A39) were the only individuals of this species collected on the reservation.

Gastrocopta procera (Gould)

G. procera is an eastern American species, common in all but the extreme western counties of Kansas. It seems to be able to survive more adverse conditions than many other gastropods in the state. Leonard and Goble (1952) believe that the success of this species in Kansas is due to its ability to withstand periods of drought and high temperature. It favors hillsides and shuns extremely moist situations. Favorable habitats include timbered areas, both in upland and flood-plain situations, as well as grasslands (Leonard, 1959), and it is frequently found beneath leaves and about old logs (Baker, 1939).

This was one of the most common snails on the reservation, collected at 13 of the 16 terrestrial stations. It seemed to be most abundant on the west-facing slope (B26) where 109 specimens were recovered. This was one of the shells commonly found in dry conditions on the open prairie, and was frequently associated with *Pupoides albilabris*. *G. procera* seemed to favor fairly dry environments since it was not abundant in the more mesic areas of the hedgerows and woods. Shells were generally collected under limestone rocks and cow dung, although many were found buried among the roots of prairie grasses.

Gastrocopta cristata (Pilsbry and Vanatta)

This snail is usually found associated with *G. procera* on timbered slopes near streams (Franzen and Leonard, 1947). One dead shell, probably of this species, was collected in the woods area in A21. The shell lacked the bifid lamellae of typical *G. procera* although there is a possibility that it was an immature specimen.

Gastrocopta tappaniana (C. B. Adams)

This common Kansas snail is found over much of eastern North America with the exception of the southern Atlantic coast states. Its most frequent habitat is on shaded slopes near streams (Franzen and Leonard, 1947). Both Baker (1939) and Leonard (1959) list favorable habitats for *G. tappaniana* as pieces of wood, logs, and damp debris in moist places.

Ten shells of this species were collected under rocks around the spring (A39), and nine dead shells were collected under decaying logs in the wooded area of A21.

Pupoides albilabris (C. B. Adams)

This widely distributed snail is found over much of the state although records are lacking for the extreme western counties. Like *Gastrocopta procera*, with which it is frequently associated, *P. albilabris* seems to be adaptable to a variety of conditions. Although Archer (1939) writes that this species apparently does not occur in woodland

cover, Leonard and Goble (1952) report that it is found in woodlands as well as in open country. It lives under stones or at the roots of grass in well drained but often sunny places. Following rains it is sometimes found a few feet from the ground on trees (Pilsbry, 1948). Leonard (1959) finds *P. albilabris* tolerant to arid conditions and high temperatures and says it is often found under sticks, logs, and litter in wooded areas, as well as in drier situations such as open pastures. Its common habitats include wooded bluffs and hillsides by rivers and streams (Baker, 1939).

We found this species to be the most widely distributed snail on the reservation, but it was not as abundant as *Gastrocopta armifera* or *Vallonia parvula*. It was collected at 15 of 16 terrestrial stations with the largest number of individuals being found under limestone rocks in a prairie wash (B4). This was the most common snail in extremely dry conditions on the open prairie, often occurring among the roots of grasses.

Succinea sp.

This family is worldwide in distribution with species most numerous in America, southern Asia, Hawaii, and Europe. The usual habitat of the genus is on plants growing in or near the water (Leonard and Goble, 1952).

Succinea occurred over most of the reservation. Fourteen different collection areas provided shells of this snail, although most of them were dead. Reeds and grasses near or in the water at the spring and the undersides of rotting logs and leaf litter were the best collecting areas.

Vallonia parvula (Sterki)

According to Taylor (1960), this species occurs on the Great Plains from South Dakota to north-central Oklahoma; eastward to northern Missouri, northern Ohio, southern Ontario, and western New York. The species is generally distributed over Kansas, but is absent from the southwestern counties.

Most surveys indicate the *V. parvula* prefers woodlands. Leonard (1959) gave wooded areas in upland and floodplain situations as favorable localities. Baker (1939) found the habitat to vary from woodlands adjoining small lakes to bluffs of rivers, while Franzen and Leonard (1943) reported this species as occurring under logs or stones where there is considerable moisture, although it will survive arid periods. In northern Nebraska, *Vallonia parvula* occurs under logs, bark, and stones on slightly moist leaf mold in wooded areas (Taylor, 1960). A Leonard (1943) characterizes this snail as highly successful in the arid conditions of western Kansas.

The Ross Reservation survey tended to verify the above observations. *Vallonia parvula* was collected at 8 of 16 terrestrial stations, but was completely absent on the prairie and other extremely dry areas. Most of the shells were collected in hedgerows (B1-B16) and under the limestone ledge (C33). Shells were usually collected in loose leaf

mold and in soil under hedgerows and limestone outcrops, although a few were found under rocks.

Helicodiscus parallelus (Say)

This species occurs in Kansas as far west as Meade County (Leonard and Goble, 1952), and also over much of the northeastern United States. This is a forest snail living on decaying wood or damp leaves in shady or humid places (Pilsbry, 1948). Its most natural habitat is in wooded river valleys or in floodplain areas (Baker, 1939). In more arid parts of the state of Kansas this snail is limited to woodland cover and usually occurs in decaying timber (Leonard and Goble, 1952).

Only dead shells of this species were collected on the reservation. Several badly weathered shells were found in loose soil under the limestone ledge (C33) and most of the other shells came from debris and leaf litter in the hedgerow (A42-A39) and the wooded area (A21).

Helicodiscus singleyanus singleyanus (Pilsbry)

An eastern American species, this snail is generally distributed over the eastern two-thirds of Kansas. It has apparently never been collected alive in the High Plains. In southwestern Kansas fresh shells have been found by University of Michigan field parties in the course of collecting fossils by washing matrix through screens. It seems probable that *H. singleyanus* lives among grass roots, even on exposed slopes that become hot and dry during the summer (Taylor, 1960). It is usually found under forest debris or among leaves or piles of washed materials (Baker, 1939).

Only four specimens were collected in this study. These shells, all dead, came from siftings of debris and loose soil in the wooded area (C33), hedgerow (B1-B16), and prairie area (A6).

Stenotrema leai aliciae (Pilsbry)

At the present time this species is limited to the eastern section of Kansas. It forms part of a series of closely intergrading forms found over much of eastern North America. Leonard (1959), Leonard and Goble (1952) and Pilsbry (1940) record this snail as an inhabitant of moist or very humid areas. Franzen and Leonard (1943) write of it as distinctly a woodland snail in northeastern Kansas.

Our findings tend to substantiate these statements. In all cases, this species was collected on the reservation in wooded or shaded areas having a fair amount of moisture. It was most common around the limestone ledge in C33, but was not abundant anywhere. At the five stations where this species was collected, shells were found under decaying logs, in leaf mold and in other decaying plant parts.

Bulimulus dealbatus (Say)

Our study area is near the northeastern limit of distribution for this tropical American family. *B. dealbatus* is a colonial snail, usually

found in open, arid country. Populations usually occur on summit areas, often on bluffs along rivers, and hibernate by burrowing in soil (Leonard and Goble, 1952).

Only three dead shells of this species were found on the reservation. These were collected on the dam of a small pond in A5. We are not sure how they got there.

Hawaiiia minuscula minuscula (Binney)

This small mollusk has followed the paths of man throughout much of the world. Although it can withstand arid conditions, it is most abundant in wooded places where moisture conditions are better than on the treeless prairies (A. Leonard, 1943). Baker (1939) and Leonard and Goble (1952) also named wooded areas as the most favorable habitat for this species. The snail may be found under logs, sticks, stones and clumps of grass in floodplain and upland situations, and it seems to thrive in piles of moist drift that have been cast by floodwaters (Franzen and Leonard, 1943).

Although *H. minuscula* was not abundant on the reservation, it was found in dry as well as in moist situations. The greatest number were collected under rocks around the spring (A39) and under logs in the wooded area (A21), but shells were also found on the relatively dry prairie (B35) and west-facing slope (B26). Specimens were usually found under rocks, logs, and loose soil at the collecting points.

Retinella indentata (Say)

This species is limited to the eastern third in Kansas, which marks its western boundary in North America. It is found along river valleys, in wooded areas and in former prairie lands (Baker, 1939), usually occurring on timbered slopes under stones, logs, loose bark, and debris. It is rare in open country, although it occurs on rocky slopes having sparse cover, according to Leonard and Goble (1952).

Fitch and Lokke (1952) found *Retinella indentata* well represented on the University of Kansas Natural History Reservation, but it was less abundant than *Retinella electrina* in moist woodlands. It is usually found associated with *Zonitoides arboreus* and *R. electrina* (Franzen and Leonard, 1943).

This species was not as common as *Zonitoides arboreus* on the Ross Reservation. It was found at three terrestrial stations, and two dead shells were taken from gravel screenings on the bottom of the stream (B48-A21). Here also, it was usually connected in conjunction with *Z. arboreus*. It was collected from moist areas only, with the largest number found under moist leaf mold in a hedgerow (A42-A39). This species was often found under or on rotting wood or in moist leaf litter.

Zonitoides arboreus (Say)

This snail has been introduced into many parts of the world, and is found over the North American continent. It is distributed over the eastern half of Kansas. Pilsbry (1946) found it to be abundant

wherever there were trees or shelter of any kind in the eastern states in the Mississippi valley. He stated that it can be found under bark, boards, bricks, or stones, or any like situation offering protection from the sun, with sufficient moisture. In northern Nebraska, it was found under logs and bark and among leaves on damp ground, usually in wooded areas (Taylor, 1960). Rotten wood is an ideal place for this species.

Zonitoides arboreus was found in the more humid areas on the reservation, including the spring (A39), the two wooded slopes, the hedgerow (A42-A39), and a rotten log. It was not found at any of the drier situations and was almost always collected under logs or sticks or other places where moisture was abundant. From one small rotten log, 191 specimens were taken.

Sphaerium sp.

This genus is found in rivers, ponds, and lakes, usually on the surface or buried at various depths in soft mud (Baker, 1928). In Kansas, *Sphaerium* is more commonly found in streams than in ponds (Leonard and Goble, 1952).

These small clams were found in the smaller of the two ponds in A5. A few living specimens were found on the mud bottom near the pond's edge and many dead shells were found around the edges of the pond.

Unio merus tetralasmus (Ward)

This species is able to dig into the mud bottoms of ponds or streams to a depth of a foot or more and is thus able to "hibernate" during dry periods (Baker, 1928a). This is a common mussel in ponds and other water bodies in Kansas.

Three dead shells of this species were picked up on the edges of the larger of two ponds in A5. No living specimens were found.

CHECK LIST OF THE MOLLUSCA OF THE ROSS RESERVATION

Phylum Mollusca

Class Gastropoda

Order Pulmonata

Suborder Basommatophora

Family Physidae

Physa hawnii Lea

Family Planorbidae

Helisoma trivolvis lentum (Say)

Family Lymnaeidae

Lymnaea bulimoides techella (Haldeman)

Suborder Stylommatophora

Family Pupillidae

Gastrocopta armifera (Say)

Gastrocopta contracta (Say)

Gastrocopta pentodon (Say)

Gastrocopta procera (Gould)

Gastrocopta cristata (Pilsbry and Vanatta)

- Gastrocopta tappaniana* (C. B. Adams)
- Pupoides albilabris* (C. B. Adams)
- Family Succineidae
- Succinea* sp.
- Family Valloniidae
- Vallonia parvula* Sterki
- Family Endodontidae
- Helicodiscus parallelus* (Say)
- Helicodiscus singleyanus singleyanus* (Pilsbry)
- Family Polygyridae
- Stenotrema leai aliciae* (Pilsbry)
- Family Bulimulidae
- Bulimulus dealbatus* (Say)
- Family Zonitidae
- Hawailia minuscula minuscula* (Binney)
- Retinella indentata* (Say)
- Zonitoides arboreus* (Say)
- Class Lamellibranchia
- Order Schizodonta
- Family Unionidae
- Uniomereus tetralasmus* (Ward)
- Order Heterodonta
- Family Sphaeriidae
- Sphaerium* sp.

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Indication of the Sense of Smell in the Turkey Vulture, *Cathartes aura* (Linnaeus), from Feeding Tests

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ABSTRACT: Two turkey vultures, *Cathartes aura* (Linnaeus), were employed in a series of feeding trials. Birds were presented individually with leaf-filled pans in one of which meat was concealed from view. Pans were presented in the open, concealed from direct view behind screens, or concealed in boxes with single openings. In each type of feeding trial pans with food were selected first a significant number of times. Evidence of a sense of smell is believed afforded. Interpretations of results suggest that smell may be of a degree of importance varying with the situation confronting the bird. Preference for freshly-killed chicks over other types of fresh and decaying meat was shown. Various observations of the behavior of the captive birds are included.

Importance of the olfactory sense in the orientation of feeding activities of birds is poorly understood. Relative importance of the exteroceptors functional in food-finding by carrion-eating birds has long been of particular question. There seems to be little, if any, conclusive evidence that a sense of smell even exists in such species. The purpose of this investigation was to determine by means of feeding experiments whether a sense of smell could be demonstrated to exist in the Turkey Vulture, *Cathartes aura* (Linnaeus).

Literature pertaining to the possibility of olfaction in the Turkey Vulture or other species of the family Cathartidae is considerable. Many of the references are confusing or of questionable scientific value. Audubon (1859: 15), Darwin (1860: 175-176), and others presented negative evidence or rejected the possibility altogether. Beebe (1909: 467) gave conflicting evidence. Indications of a sense of smell have been given by Rhoades (1883), Gurney (1922: 241), and Howell (1932: 162). Strong (1911) indicated an intact well-developed olfactory nervous system in the Turkey Vulture. Northington (1936), however, has pointed out that the functional capacity of a sensory nerve may not be proportional to the size of the associated structure.

Two Turkey Vultures, sex undetermined, were trapped alive in Dade County, Florida, during the fall of 1953. They were housed in individual compartments consisting of an outer portion measuring 5' x 5' x 8' in height, screened to the outside and provided with two perches each approximately six feet long, and a continuous inner portion of solid walls and ceiling, with dimensions of 9' x 8' x 8'. A door provided with one-way vision mirror-glass was situated in the far wall of each inner compartment.

After a period of eight weeks conditioning to confinement, controlled feeding was initiated. Canned dog food (largely horse meat),

which was allowed to putrify, was used in most feeding trials. Hatchery-obtained chicken culls, both freshly killed, and putrified, were also used.

Four types of feeding experiments were carried out. Observations of the birds after feeding pans were in position were made from outside the compartments through the mirror-glass.

Feeding experiment one.—Two identical metal pans were placed three feet apart in the center of each inner compartment. Both pans were filled with several inches of fresh dead leaves; putrescent horse meat was concealed beneath the leaves of one of the pans. In this and other experiments, relative positions of the food pans in successive feedings were rotated at random. Conditions permitting, feeding trials were made each day.

Feeding experiment two.—Two pans, which were placed approximately eight feet apart on opposite sides of the inner compartment, were concealed from direct view of the vultures by wooden screens. At the disturbance caused by placing the pans, the vultures invariably retreated to their perches. To reach the pans the birds were then obliged to pass the length of both compartments, go to one side of the inner compartment, walk around the screen and approach the pan from the side or rear. Pans were filled with dead leaves; putrescent horse meat was concealed in one of them.

Feeding experiment three.—Putrifying horse meat smeared on dead chicks was concealed in one of three identical, leaf-filled pans. Pans were placed two feet apart in line in the center of the inner compartment.

Feeding experiment four.—Each of three leaf-filled pans was placed in a wooden box provided with a three-inch diameter opening. Boxes were identical and were placed in a line, approximately two feet apart; the openings faced in the opposite direction from which the vultures approached them. The birds were obliged to thrust their heads through the opening and explore the leaf-filled pans for horse meat-smeared chick-culls.

The vultures usually hopped from their perches and approached the feeding setups within a few minutes after the disturbances incidental to pan-placing. In some instances the birds were slow to, or did not initiate food investigation during the observation period. Such instances are reflected in the data of Table I.

The initial impulse to seek food was probably a conditioned reaction involving auditory and visual stimuli connected with placing the food pans in position; in no case did this impulse arise, necessarily, from olfactory stimulation.

RESULTS AND DISCUSSION

Data obtained from the feeding experiments is expressed in Table I. These results furnish indication that the Turkey Vulture does possess a sense of smell. Results of Experiments One and Two are statistically significant. In Experiments Three and Four, χ^2 values in

the case of Vulture I, which exhibited the smallest number of correct choices, are 18.0 and 9.4; the probability (two degrees of freedom) of these feeding choices occurring by chance is less than .01 per cent.

It is to be emphasized that no attempt has been made to ascertain the importance of smell to the Turkey Vulture in locating food under natural conditions.

The functional organization of the nervous system provides a resultant response to a correlation of perceptions from stimuli of the special senses. In situations where certain perceptions are of relatively great importance to the organism, a minimal stimulus may be utilized to its fullest measure. In the Turkey Vulture, for example, the visual sense may suffice to insure the finding of food. But under varying

TABLE I.—Results of feeding experiments with two Turkey Vultures

	EXPERIMENT 1			EXPERIMENT 2		
	Bird		Total	Bird		Total
	1	2		1	2	
Number of trials	47	47	94	42	42	84
Number of trials during which feeding was begun	32	28	60	22	38	60
Number of times pan with food was investigated first	30	21	51	21	36	57
Percent of number of observed feedings in which pan with food was investigated first	93	75	84	95	94	94
Number of times pan(s) without food was (were) investigated first	2	7	9	1	2	3
Percent of number of observed feedings in which pan(s) without food was (were) investigated first	6	25	16	4	6	5
	EXPERIMENT 3			EXPERIMENT 4		
	Bird		Total	Bird		Total
	1	2		1	2	
Number of trials	55	55	110	45	45	90
Number of trials during which feeding was begun	44	46	90	44	45	89
Number of times pan with food was investigated first	28	30	58	24	27	51
Percent of number of observed feedings in which pan with food was investigated first	63	65	64	54	60	57
Number of times pan(s) without food was (were) investigated first	16	16	32	21	18	39
Percent of number of observed feedings in which pan(s) without food was (were) investigated first	36	34	35	46	40	43

situations other senses may attain prominence. Thus in certain situations the sense of smell may be of importance to the bird. In this respect the results of Experiment Two, in which the greatest number of correct choices was made by both birds, are interesting. Here pans were situated at the compartments' ends which were shunned by the birds because they contained the doors through which the investigators entered. Approach to a pan as well as escape from its vicinity was possible from but one direction. The birds' great timidity may well have resulted in greater discrimination on their part.

A sense of smell in the Turkey Vulture might also function in selection of carcasses as well as portions of a carcass. Hamrum (1953: 877) found indications that odor (and taste) may influence the food choice of the Bobwhite, *Colinus virginianus* (Linn.).

The smallest number of correct choices was made in Experiment Four, in which the pans were concealed within wooden boxes. It is not improbable that the normal diffusion of food odor was impeded by the box. Diminished olfactory stimulation may have resulted in a greater degree of exploration for food.

It may be questioned if use of but two birds affords results which are to be regarded as representative of the species. General behavior of the birds was considerably stereotyped. There is considerable uniformity in statistical comparison of their choices.

ADDITIONAL OBSERVATIONS

The vultures appeared to be in good health throughout their 18 months of confinement. However, they made little adjustment to captivity. Their escape tactics never ceased. When presence of people was realized, the birds remained poised for retreat. Constant flapping against the screen walls resulted in frayed remiges and rectrices. Water consumption appeared to be negligible; only once was a bird observed to drink. On no occasion was it observed that undigested material was regurgitated in pellet form. Frightened birds usually regurgitated any food recently taken; in most cases this was soon re-eaten.

Both vultures continuously explored their quarters and any strange objects within them. Brooms, paper cartons, pieces of paper and other materials left in the cages were scattered about and often torn to bits. Having fed, the birds would tear the leaves from the foodless pans. In this respect, attention should be called to various trials which have been made with confined vultures in which nonodorous models of animals have been employed.

The avidity of the vultures for freshly-killed chicks invited a series of feeding trials in which a choice of meats, as well as the degree of decomposition of such, could be made. A single pan with exposed food in each of its corners was presented to the birds. Food was arranged as follows: corner A, fresh canned horse meat; corner B, odorous, decaying horse meat; corner C, freshly killed chick; corner D, freshly-killed chicks smeared with odorous, decaying horse meat. Sixty

observations (thirty for each bird) were made as to the food selected first. The freshly-killed chick was selected first 45 times; the freshly-killed chick smeared with putrifying horse meat was selected first 13 times; the fresh horse meat was selected first two times; the putrifying horse meat was never selected first. A preference for fresh meat as well as a type of fresh meat, was thus indicated. This being the case, the question may well be raised concerning the use of a sense of smell in locating freshly-killed, presumably relatively nonodorous materials under natural conditions. It also suggests that a diet of carrion may, under natural conditions, not be preferential.

There are reports of Turkey Vultures attacking live animals. Hamilton (1941) noted attacks on newly born pigs, and Wayne (1910: 67) reported that they picked the eyes from a live, but mired cow or horse. Parmalee (1954: 443), reporting on depredations by vultures in Texas, concluded that most, if not all, of the live domestic animals preyed upon by vultures were attacked by Black Vultures. He pointed out that reports of similar attacks by Turkey Vultures may be based upon mistaken identification. When live chicks were released in our captive vultures' compartments, the vultures immediately retreated, although they had had much experience in feeding on dead ones. One vulture, starting to devour a dying chick, dropped it and trotted away in haste when the chick suddenly struggled.

The long-recognized importance in food location of visual cues afforded by the behavior of other vultures, as described by Meinertzhagen (1959: 127) and many others, was emphasized at the release of the captive birds at the termination of the feeding trials. Release was made on a cloudless morning at the edge of a large, unused landing mat for lighter-than-air-craft. No vultures had been observed in the vicinity. The first releasee flapped to a height of less than 50 feet and then glided to a landing approximately 100 yards distant. Within five minutes other vultures, both Turkey and Black, appeared in the area; seven were counted spiralling overhead. Three of the latter landed next to the releasee and spent several minutes walking about him. The second bird was now released. It flapped and glided to a landing approximately one mile distant. It was followed by the entire group of vultures which had gathered about the first releasee. Several of the birds landed near the second releasee and remained walking slowly about it.

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Population Structure and Reproduction in the Lizard *Uta stansburiana stejnegeri*

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ABSTRACT: Three populations of the lizard *Uta stansburiana stejnegeri* in western Texas were studied by mass sampling over a two-year period. Additional information was obtained by marking experiments in one of the populations.

The sex ratio is not significantly different from 50:50 in any population, age group or season. However, since males reach a larger size than females, samples containing predominantly large lizards may be as much as 90 per cent male.

All lizards mature at the age of one year or less. Despite differences in climatic conditions and other factors almost all lizards are reproductive during the mating season. There is an annual turnover in the population as most adults disappear at the end of their first reproductive season.

Reproductive potential is a function of size of the female and the season. Larger females produce larger clutches and clutch size is larger early in the reproductive season than later. Approximately 38 days are required from the beginning of ovarian follicle enlargement to ovulation; three clutches per year are laid by females maturing early in the season. Reproductive potential may be calculated accurately on the basis of number of oviducal eggs, number of yolk-filled follicles, or number of corpora lutea. Counts of total numbers of follicles are not useful for estimating reproductive potential.

Estimates of natality at the population level can be fairly accurately made by knowing the sizes of females in the population. This has been verified by field experiments.

Data are presented on ratio of juveniles to adults in the populations, on size and age at maturity, on testis development and regression, on corpora lutea and atretic follicles, on gonad development in juvenile lizards, seasonal cycles in the ovaries and interuterine migration of ova. Numerous comparisons are made with published data on other species of lizards.

Uta stansburiana stejnegeri, the desert side-blotched lizard is widely distributed in North America from Nevada and California to western Texas and northern Mexico (Smith, 1946). It is extremely abundant in western Texas and is more easily obtained in large numbers than most iguanid lizards. For these reasons it was chosen for sampling experiments to obtain data on reproductive cycles, population structure, and variation in morphological characteristics. The data on variation and stability of taxonomic characters will be published separately.

Acknowledgments.—I am grateful to the National Science Foundation for their support of this study and to the following students of Texas Technological College for their help in the field: Garry Knopf, Sumner Dana, Don McGregor, Johnny George, Jerry Gerald, William Voss and Don Woodard. I also wish to thank Robert G. Webb of the University of Kansas for furnishing me with some *Uta stansburiana* samples from Randall and Armstrong

counties in northwestern Texas and for his help on many field trips to that area. I am particularly grateful to Chester Rowell of Texas Technological College for his identification of certain plants.

INTRODUCTION AND DESCRIPTION OF AREAS

Many localities in northwestern and western Texas were investigated and three of these were chosen for sampling experiments. The most northerly population is at the northern extreme of the range of this lizard in Texas and lies in Palo Duro Canyon in extreme northern Armstrong County, 17 miles east southeast of Canyon, Texas. This canyon is a deep cut in the high plains of Texas with an altitude of about 3600 feet above sea level at the rim and 2000 feet or more on the canyon floor. The canyon has been cut by the aggrading Red River and, although quite rocky in places, has some considerable areas of riverborne sand on the floor. It is only in the sandy areas that *Uta stansburiana* is abundant; it does not show a preference for a rocky habitat anywhere in western Texas, but has been reported as saxicolous in some parts of its range by Smith (1946). The principal vegetation in the microhabitat is salt cedar (*Tamarix gallica*), sparse grasses, juniper, and cottonwoods along the permanent tributaries. Large piles of drift often provide a great deal of cover around the bases of these trees.

Other lizards occurring in the same habitat in order of apparent relative abundance are *Sceloporus undulatus consobrinus*, *Cnemidophorus tessellatus*, *Crotaphytus collaris collaris*, *Cnemidophorus sexlineatus*, *Phrynosoma cornutum* and *Eumeces obsoletus*.

The sampling area is characterized by hot summers, and winters during which conditions are alternately mild and rigorous. The summer temperatures are generally between 95° and 100°F; freezing occurs almost every night between November and early March. The mean July temperature is 78°F; the mean January temperature, 35°F and the length of the growing season 201 days.

The greatest difficulties in sampling were encountered in this northern population. Periodic flash rainstorms characteristic of this area of Texas send walls of water down the narrow canyon floor which often completely change the microhabitat, disrupting home ranges and washing away egg-laying sites. For this reason a second sampling area was chosen in Armstrong County on the Hedgecock Ranch, 19 miles southwest of Claude. This second station is about 20 miles south of the first in a similar habitat. An extremely devastating flood in July, 1960, almost destroyed the lizard population at both stations.

The two southern study areas are 250 airline miles south of Armstrong County on the sandy mesquite plains at an altitude of about 2800 feet. One of the areas is located 6 miles south of Kermit, Winkler Co.; the other, 11.5 miles south of Monahans, Ward Co. The principal vegetation in both areas is a low shrubby mesquite (*Prosopis glandulosa*) with large intervening areas of loose sand supporting clumps of broom weed (*Xanthocephalum sarothrae*), sand

sage (*Artemisia filifolia*), allthorn (*Koberlinia spinosa*), huisache (*Mimosa* sp.) and beargrass (*Yucca angustifolia*).

The only other abundant lizards in these areas are *Cnemidophorus tigris*, *Phrynosoma cornutum* and *Crotaphytus wislizeni*.

The two southern populations are characterized by extremely hot summers and mild winters. The daily temperature in the summer is usually 100°F or higher. Sand temperatures taken daily in the summer at the Winkler County station were usually above 130°F with a difference of 60°F between maximum and minimum readings. The mean July temperature in the area is 82°; the mean January temperature, 46°; and the length of the growing season, 218 days.

Between the northern and two southern populations is a large area rather unfavorable for *Uta stansburiana* so that the northern population is partially isolated from the southern ones.

PROCEDURE

An attempt was made to get monthly samples from each of the three populations. This was possible in every month but December and January in the southern populations. Large samples were extremely difficult to obtain from the northern population at any time, but particularly during the winter. During the reproductive season in spring and summer, samples were collected more frequently. In all, 86 samples were collected; 33 from Armstrong County, 31 from Winkler County and 22 from Ward County.

Sampling was begun in the winter of 1958 and carried through the summer of 1960. A few samples were collected from the northern population prior to 1958 and the data from these specimens have been used in this paper where appropriate. In all, 416 specimens were obtained from Armstrong County, 616 from Ward County, and 875 from Winkler County, a total of 1907.

The specimens were usually preserved within four to six hours after capture. Sex in all lizards was determined by dissection although sex can be determined with a high degree of accuracy by the presence of enlarged postanal scales in males. Measurements of body length and of eggs or large ovarian follicles were made to the nearest millimeter with dividers while smaller follicles (5.0 mm or less) and all testes were measured to the nearest 0.1 mm with an ocular micrometer.

In addition to data obtained from samples, some important data on subjects discussed in this paper were obtained from marking experiments with *Uta stansburiana* in a 10,000 square yard quadrat area near the Winkler County sampling area. This marking study was begun as a part of a project studying the effects of radiation on a natural population of lizards supported by the U. S. Atomic Energy Commission.

POPULATION STRUCTURE

Sex Ratio

Sex could be determined in almost every specimen. Only in hatchlings that had been damaged internally was sex not determined.

Sex in adult lizards can be easily distinguished at a glance for there is strong sexual difference in pattern with the females being striped and drab, while males are unstriped and brightly colored with blues of various shades during the spring and summer. The ratio of all samples combined was 943 females to 945 males, almost exactly the expected 50:50.

The ratios are also not significantly different from 50:50 in any of the three populations. The percentage of 413 from Armstrong County was 49.4 per cent female; of 860 from Winkler County, 50.8 per cent female, and of 615 from Ward County, 49.1 per cent female. None of these data indicate that males are less easily captured than females because of a difference in habits as suggested by Smith (op. cit.), nor has this been my impression in the field.

The samples were also compared on the basis of season and of size groups of lizards. There are deviations from a 50:50 ratio in some of these seasonal groupings, but usually when the sample size is insufficiently large to be unbiased. Occasionally, deviations do occur in large samples, but these are still attributable to sampling errors. For example, during egg laying, females tend to stay near cover such as pack rat nests and males may thus be obtained in greater numbers.

The sex ratio at birth is difficult to ascertain from samples alone. The size at hatching is between 20 and 25 mm body length. The sex ratio of 126 lizards less than 30 mm and hence in their first few weeks of life is 52 per cent male, 48 per cent female. The ratio of 1009 known adults is 51 per cent male; 49 per cent female indicating close agreement and little ontogenetic change.

The sex ratio does change in different size groups of adults. This may be illustrated with the samples from Ward County. In the size group (arbitrarily selected) 41-50 mm there are 219 adult females and 116 adult males for a 65:35 ratio, while the ratio for 100 lizards in the group 51-60 mm is 6 females:94 males. The preponderance of males in the larger group is due to the fact that males attain a larger size than females. Note that the sex ratio of the total is 50:50.

Sex ratios of lizards marked in the Winkler County study area during the summer of 1960 may be indicative of the actual sex ratio. Of 111 juveniles marked in which sex could be determined with certainty, 59 were females and 52 males. Of the adults, 25 were females and 20 males. The difference in juveniles is insignificant, but is opposite to that obtained by sampling. The deviation from expectation in the adults is due to strong male rivalry in this species in which territories are discrete. Although another male will not be tolerated, one male may have more than a single female within his territory.

Ratio of Juveniles to Adults

For this comparison, the year was divided into four periods of three months each: January to March when females are developing large ovulatory follicles, April to June when most reproduction occurs, July through September when reproduction is completed and most

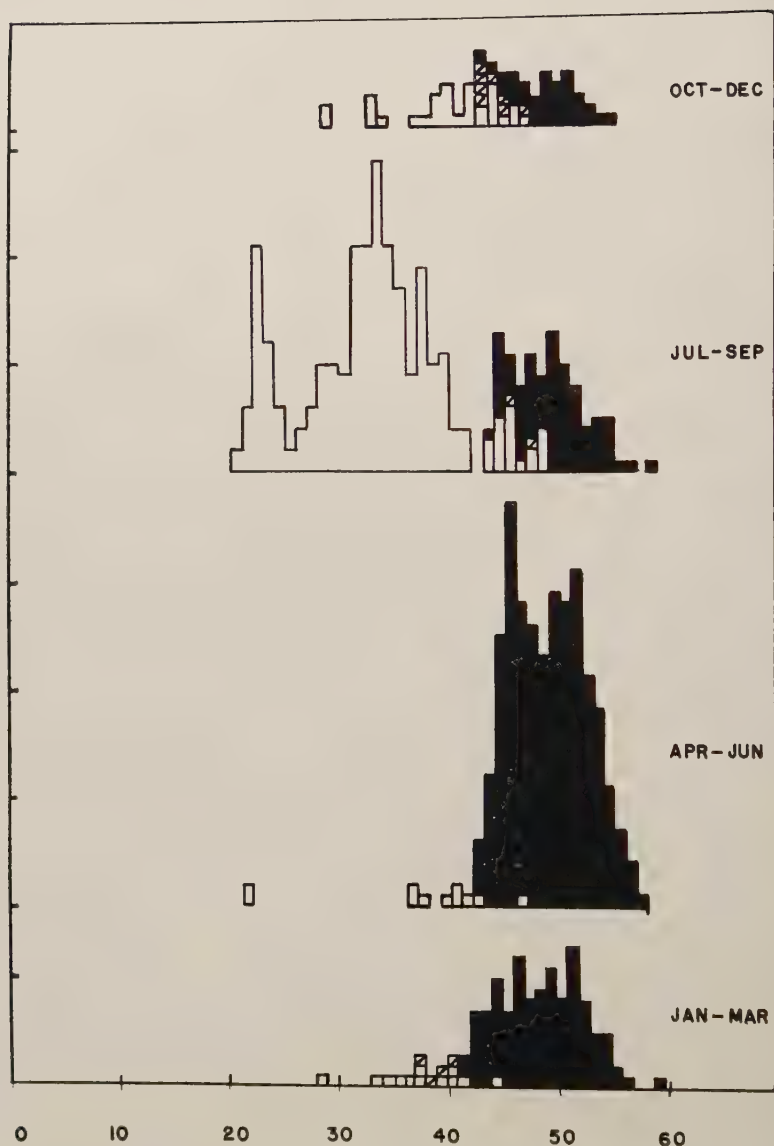


Fig. 1.—Histogram showing number of individuals of each size in *Uta stansburiana* in Winkler County, Texas, in four seasons. Abscissa: Body length in mm; ordinate: number of individuals. Each mark (other than those showing base lines) is 10 individuals.

hatchlings appear, and October to December when the gonads are quiescent and young lizards are reaching adult size. All periods, naturally overlap to some extent. The data for all years for which samples were available were combined. The distribution of size groups of lizards in each of these four periods is shown in Figures 1-3 and in different form in Table I.

It is apparent that most juveniles appear in all three populations in the period July to September with the peak number appearing in July and early August. The difference in the percentages of juveniles

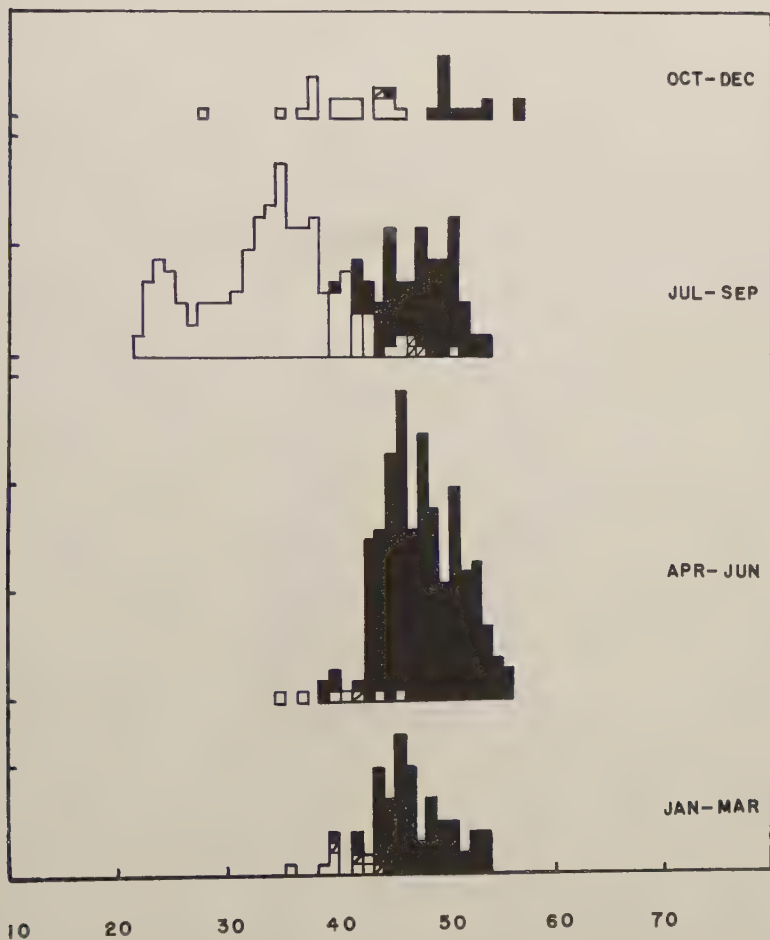


Fig. 2.—Histogram showing number of individuals of each size in *Uta stansburiana* in Ward County, Texas, in four seasons. Abscissa: Body length in mm; ordinate: number of individuals. Each mark (other than those showing base lines) is 10 individuals.

to adults during this period cannot be explained on the basis of available data.

Many of the juveniles reach mature size (40-45 mm) by the end of the summer during which they hatch. That some late season hatchlings were still quite small the following year is clear from the

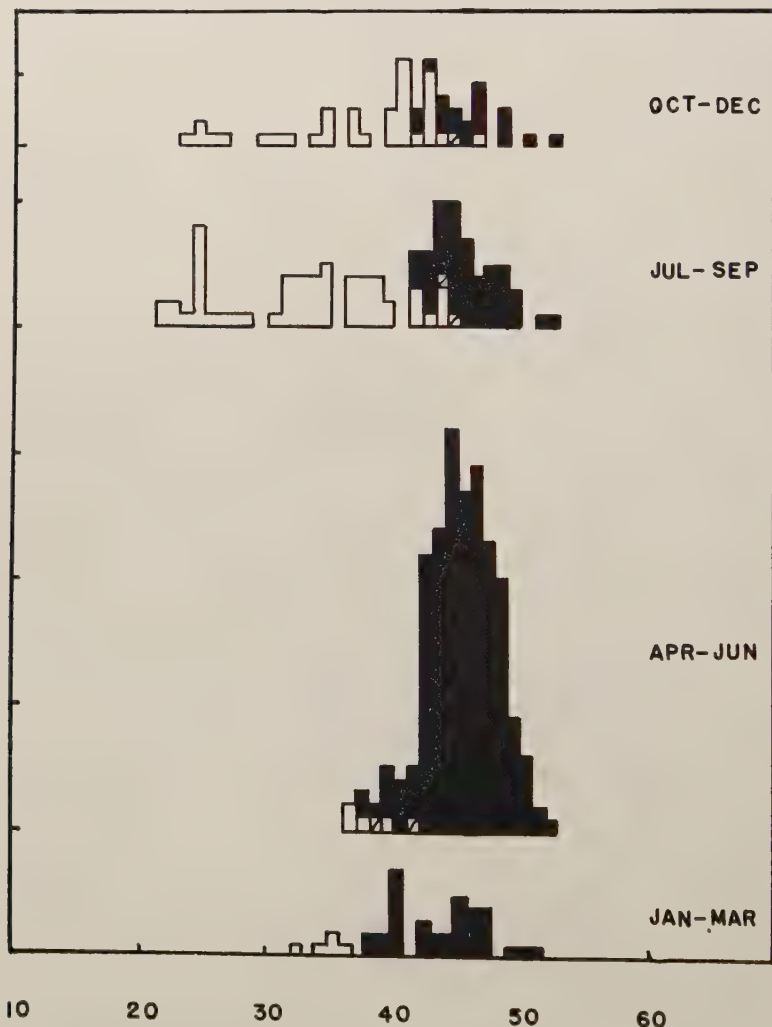


Fig. 3.—Histogram showing number of individuals of each size in *Uta stansburiana* in Armstrong County, Texas, in four seasons. Abscissa: Body length in mm; ordinate: number of individuals. Each mark (other than those showing base lines) is 10 individuals.

fact that there are lizards between 30 and 40 mm in length in each population in January-March. In fact, one specimen measuring only 22 mm was recorded in the Palo Duro population during this period. Such a small individual may have been hatched late the previous year and may not have grown at all the succeeding few months or it may have hatched from an egg that overwintered. The idea that many lizards reach adult size in the same summer they hatch has been verified by periodic measurements of marked hatchlings.

There is a greater percentage of juveniles in the October to December samples from Armstrong County than in the other two populations (Table I). This is what would be expected in the northern population because of its earlier winters and consequent shortening of the growing season. Too, hatching of the first clutch of eggs is probably generally later in the northern population than in the southern ones, so that few individuals can reach mature size by the end of the summer. This conclusion is substantiated by the figures that show a decrease in percentage of adults from July-September to October-December. If many juveniles were reaching mature size an increase should be expected in the later period and such an increase is evident in the Ward-Winkler populations.

The most significant point in these data is the indication that regardless of the relative percentages of adults and juveniles at any other season, almost all lizards in all three populations are mature in April-June, and the majority by January-March. These data demonstrate that nearly every lizard is potentially reproductive at an age of 10-12 months. Although some lizards mature only a few months after hatching, none will reproduce during their first season.

The relative percentages of mature and immature lizards in July-September must be discussed in greater detail. There is likely more error in these figures than in others because it is difficult to separate old adults from subadults hatched during that summer. Therefore,

TABLE I.—Percentages of juveniles and adults at different seasons in three populations of *Uta stansburiana* (figures do not add to 100 per cent because maturity could not be determined in some specimens)

	January-March		April-June		July-September		October-December	
	Juve-niles	Adults	Juve-niles	Adults	Juve-niles	Adults	Juve-niles	Adults
Armstrong Co. N = 416	12.8	87.2	1.9	97.2	51.9	46.2	63.6	34.5
Winkler Co. N = 870	8.5	88.4	3.2	96.8	77.1	22.3	43.7	46.5
Ward Co. N = 604	7.3	89.0	2.3	96.4	66.9	32.0	52.9	44.1

the percentages of mature individuals may be too high. This possibility was investigated by comparing the number of adult lizards marked in a study area during June and July with the number of these "old" adults remaining in August and September. By mid-July every adult lizard in the study area had been marked and 23 of these were captured at least three times and must be considered residents of the area. By mid-August only 10 of these were still present in the area and in mid-September, only four. Areas adjacent to the study area were thoroughly investigated, but none of the lizards captured was marked. During the same period, the total number of lizards in the study area increased greatly and by mid-September some young lizards marked in June and July had reached or were nearing adult size. These data suggest a nearly complete annual turnover in the lizard population. Thus, data on relative abundance of juveniles and adults obtained from mass sampling during late summer and early fall are seen to be unreliable, at least if maturity is based upon criteria used by me and if there was not exceptionally greater mortality of marked lizards.

Size at Maturity, Average Size and Size Maxima

The females in all three populations may mature at a smaller size than males, but the difference in minimum size at maturity is a matter of only a few millimeters. It is easiest to be certain of maturity or immaturity during April-June because during this period yolk deposition, ovulation, or oviposition is occurring in females and enlargement of testes and vasa deferentia in males. Comparable data on sizes are shown below for the three populations:

	Minimum size at maturity	Average size of adults (April-June)	Maximum size of adults
Armstrong	38	45.9	53
Winkler	42	49.4	60
Ward	39	48.0	57

Although there are not great differences in these sizes, the smaller average size in the Armstrong County population reflects a rather striking difference in the distribution of size groups in this population. Most adults (91.7%) in the northern population are between 40 and 50 mm in body length while a smaller percentage is restricted to these limits in Winkler (59.4%) and Ward (70.5%) county populations. If there is an annual turnover of most adults in each population, this difference is to be expected because the shorter growing season in Armstrong County permits fewer individuals to reach the maximum size achieved by lizards in the other populations.

Most lizards studied reach sexual maturity rapidly, in many cases in the spring following birth the previous summer as is true in *Uta stansburiana*. Age at maturity has now been estimated in several species of North American lizards and these data are shown in Table II.

TABLE II.—Age at sexual maturity in 12 species of North American lizards

Species	Author	Age at Maturity (in years)
<i>Cnemidophorus sexlineatus</i>	Fitch (1958)	2
<i>Cnemidophorus tigris</i>	Tinkle (1959)	2-3-?
<i>Anolis carolinensis</i>	Gordon (1956)	1 or less
<i>Holbrookia texana</i>	Cagle (1950)	1
<i>Sceloporus undulatus</i>	Crenshaw (1955)	less than 1
<i>Sceloporus olivaceus</i>	Blair (1960)	1
<i>Crotaphytus collaris</i>	Fitch (1956)	2
<i>Neoseps reynoldsi</i>	Telford (1959)	1
<i>Eumeces fasciatus</i>	Fitch (1954)	2
<i>Eumeces skiltonianus</i>	Rodgers & Memmler (1943)	3
<i>Eumeces septentrionalis</i>	Breckenredge (1943)	in 3rd year
<i>Eumeces obsoletus</i>	Fitch (1955)	most 3; some 2

It can be seen that iguanid lizards studied mature within their first year, usually during their second growing season. Some may reach adult size the same year that they are hatched. The growth rate of scincid lizards is apparently slower and attainment of maturity is much slower despite the fact that as a group these species are not as large as the iguanids.

REPRODUCTIVE CYCLES

Counts and measurements of ovarian follicles of female lizards during each month have allowed formation of the composite descrip-

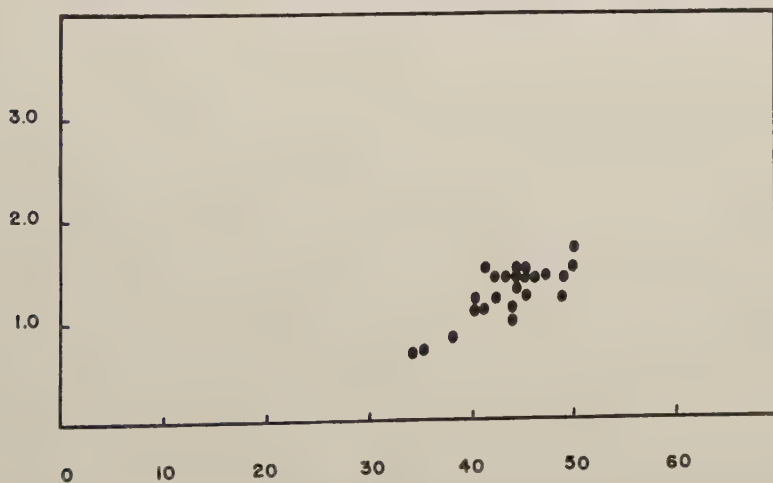


Fig. 4.—Size of largest follicles in ovary of *Uta stansburiana* in October to December. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

tions of testis and ovarian development at each season. Unless otherwise stated all references are to adults. Since the development of the gonads is similar in each population and from year to year, the data in the graphs are of lizards from the Winkler County population obtained during 1959.

Winter Gonads (October to December; Figs. 4 and 5)

During this period, distinct size groups of follicles are not present in the ovary so that it cannot be said with certainty which follicles represent the first clutch for the following spring. The follicles are all pearly white or almost clear and the maximum size of follicles is 1.7 mm, but most of the largest ones are 1.5 mm or less and seldom less than 1.0. Miller (1948) reports that follicles in *Xantusia vigilis* are similar to those that I have reported in *Uta stansburiana* and are a maximum of 1.3 mm in diameter. However, according to Miller (1951) an ovum of this size has required two years to reach that

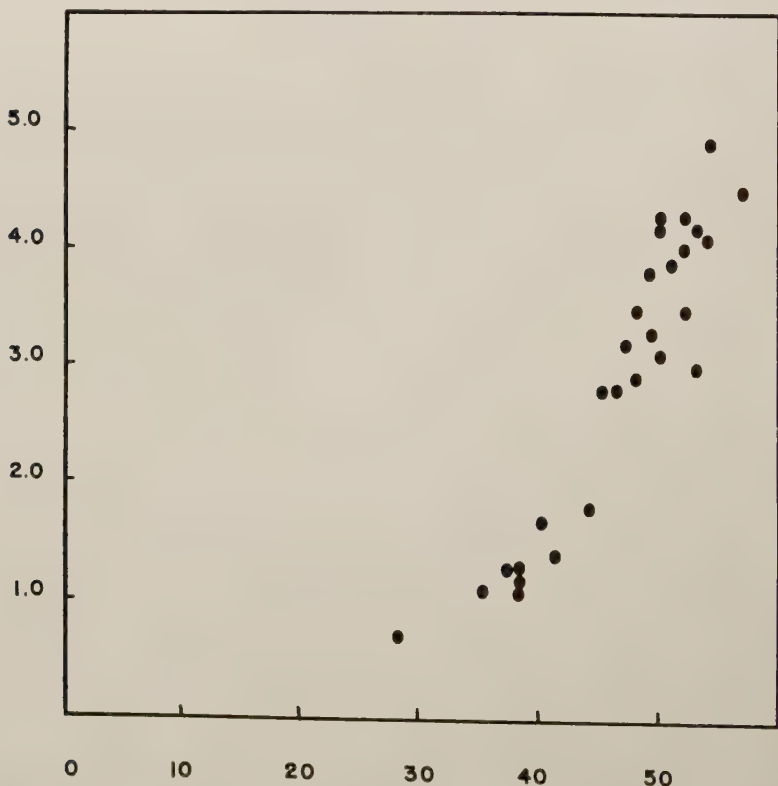


Fig. 5.—Maximum length of testis of *Uta stansburiana* in October to December. Abscissa: body length in mm; ordinate: size of testis in millimeters.

mature and subadult males are not distinctively different. Many of the males have very small testes and are obviously immature, but others have testes between 2.0 and 3.0 mm in greatest length, a size to which the testes of adult males may have regressed by this time. Macroscopic examinations of the vasa deferentia are likewise uninformative. Figure 5 does show a separation of males into two fairly distinct groups at this time, but I am not certain that all those in the larger group are adults, although it does seem likely that those in the smaller group are young of the year.

Transitional and Spring Gonads (January to March; Figs. 6 and 7)

The conditions described in the winter ovary are carried into February. The first clear changes in the gonads occur in February or March (see section on reproductive potential) depending upon weather conditions. During this period almost every ovarian follicle that has reached a size of 1.6 mm or greater will show signs of yolk deposition. The follicle first appears cream-colored and more opaque,

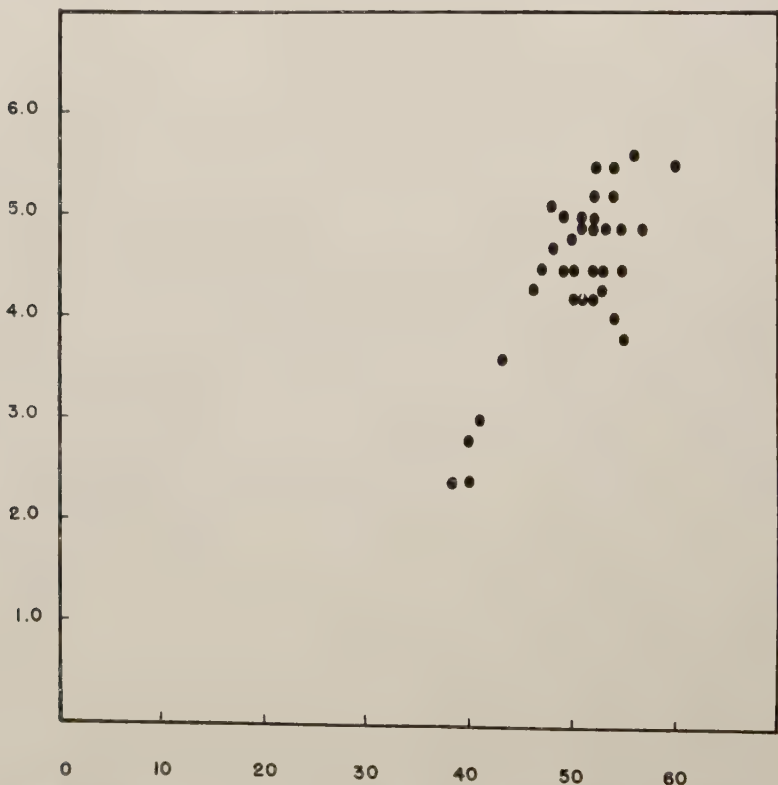


Fig. 7.—Maximum length of testis of *Uta stansburiana* in February to March. Abscissa: body length in mm; ordinate: size of testis in millimeters.

but by the time it has enlarged to 2.0 mm it will appear yellow due to increased yolk content. The yolked follicles are soon clearly distinct from others and accurate estimates of clutch size can now be made by counting them. The largest follicle seen in any population in February was 2.8 mm. In March the yolked follicles increase rapidly in size to a maximum of 8 mm. As most of the largest follicles seen in the ovary are nearer 7 mm, it is assumed that ovulation occurs at this size. This is the same size at which ovulation occurs in *Xantusia*

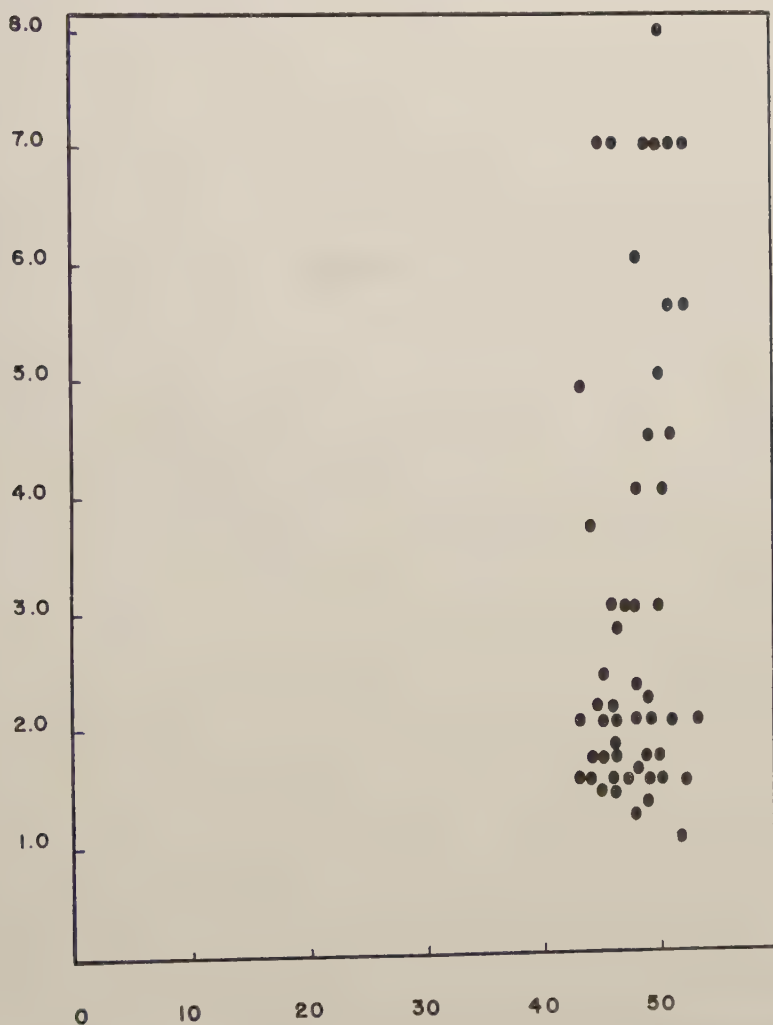


Fig. 8. Size of largest follicles in ovary of *Uta stansburiana* in April to May. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

vigilis (Miller, 1948), and in *Sceloporus graciosus* (Woodbury and Woodbury, 1945) but this is by no means constant as ovulation may occur at a larger size (10 mm) as in *Amphibolorus muricatus* (Weekes, 1934) or a smaller one (5 mm) as in *Scincella* (= *Lygosoma*) *laterale* (Johnson, 1953).

The first oviducal eggs were noted in the sample of March 8, 1959, in Ward and Winkler counties, but not until April 3 in Armstrong County. However, some females in Armstrong County might have ovulated previous to April 3 as no samples are available from March 13 until April 3. No yolked follicles were present in females of the March 13 sample from Palo Duro which would indicate that ovulation would be primarily in April. In 1960, no ovulation had occurred in females of the two southern populations as late as April 1, but had occurred when the next sample was taken on April 16. Thus, first ovulation was a month later in 1960 than in 1959. By March 27, 1960, only three females examined from Armstrong County

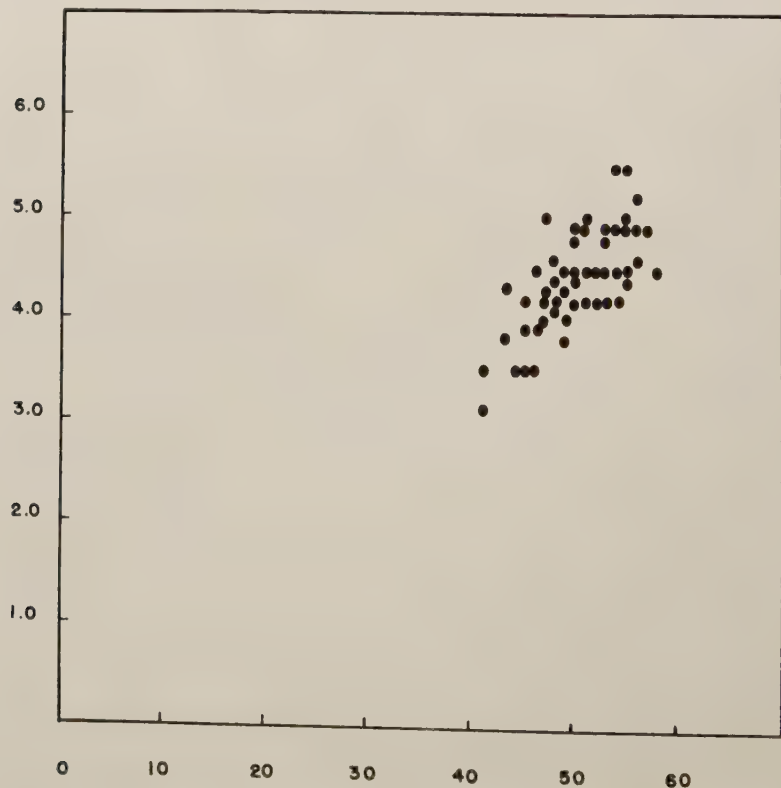


Fig. 9.—Maximum length of testis of *Uta stansburiana* in April to May. Abscissa: body length in mm; ordinate: size of testis in millimeters.

showed any sign of yolk development. Two of these had largest follicles of 2.0 mm and the third, 4.0 mm. It is doubtful that ovulation in 1960 could have occurred prior to mid-April or later. A large sample from this population on April 25 contained several females containing oviducal eggs.

In males the testes and vasa deferentia begin enlargement during this period and become sexually potent. At this time the testes have a compact appearance rather than the flatness often characteristic of winter testes. The vas deferens is tortuously convoluted and expanded by increase in size of the epithelial lining. As can be seen from Figure 7, the testes of almost every male are between 4.0 and 6.0 mm in greatest length. The only smaller ones belong to lizards hatched late the previous summer that have not yet reached mature size.

Reproductive Gonads (April-June; Figs. 8-9)

Most reproduction in these lizards occurs during this period. The testes get no larger than in the previous period, but the tubules of the testes become large and are easily seen through the enveloping tissues.

The ovary goes through a series of cycles like that described in the previous period. After the first and second ovulations, the development of another set of follicles toward ovulation begins. In no instance was a smaller set of follicles beginning yolk deposition prior to ovulation of the previously enlarged ones. This seems to be typical of most lizards, but not of all. Weekes (1934) reports that ovarian follicles in *Amphibolurus muricatus* reach one-half ovulatory size before the first eggs ovulated are laid. It is rare for *Uta stansburiana* to show any follicle enlargement or yolk deposition as long as oviducal eggs are present. The largest follicle seen in a female with eggs was 2.2 mm, but in almost all individuals the maximum is 1.5 mm with no trace of yolk deposition. That yolk deposition and enlargement proceed immediately after oviposition is clear from the observation that females with distinct corpora lutea indicating recent ovulation usually have some follicles developing yolk even though they are always less than 2.0 mm.

The Late Reproductive and Postreproductive Gonad (July-September; Figs. 10-11)

During this period the vasa deferentia of the male again became more translucent due to regression of the lining epithelium and the testes lose their rounded appearance and become smaller. Few testes exceed 3.0 mm during this period. It is likely, as noted earlier, that most of these individuals are young of the year, but doubtless there are some old adults in the group in which the testes have receded. It is clear from the figure that there are not two distinct groups of lizards with regard to size at this time.

In 1959, most egg laying ceased in July in all three populations.

Only two gravid females were seen in August, one in Armstrong County, the other in the southern populations. It is doubtless these late laying females that produce the young which appear as very small individuals in samples made early the next year (Figs. 1-3). In 1960, only one gravid female was seen in August, this in the southern populations.

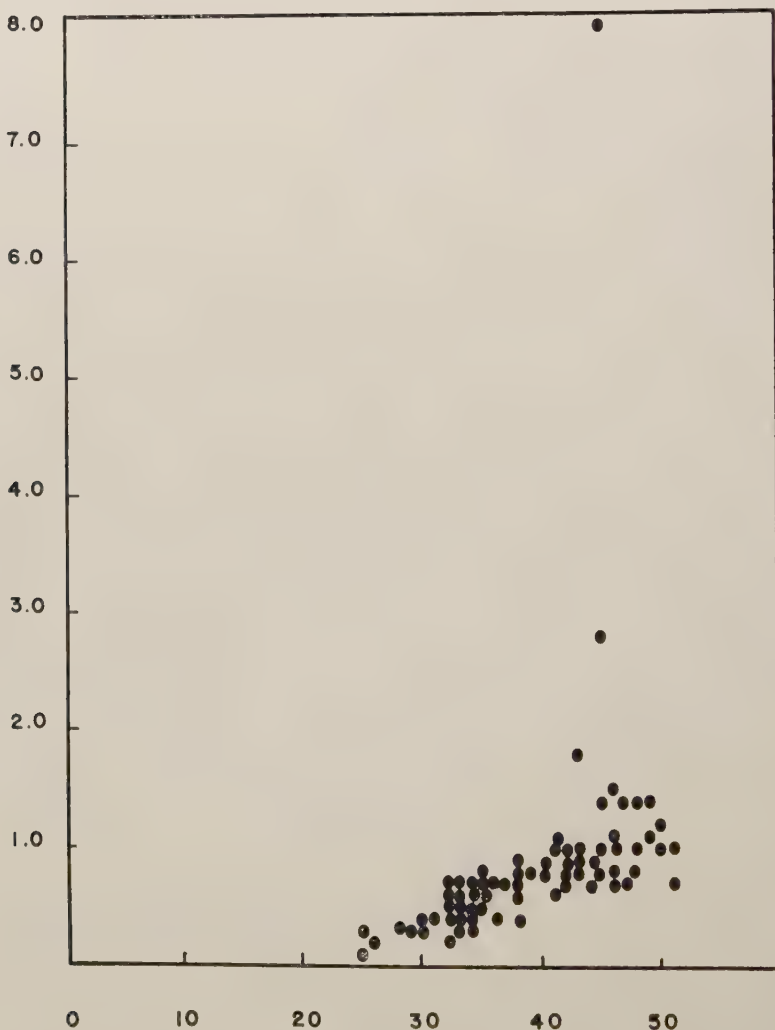


Fig. 10. —Size of largest follicles in ovary of *Uta stansburiana* in August to September. Abscissa: body length in mm; ordinate: size of follicles in millimeters.

Juvenile Gonads

Juvenile lizards appear in the populations primarily in July and later, although occasional individuals hatch in June. The sexes at hatching can generally be distinguished because follicles can be seen in the female gonad. Even when the ovary has not differentiated, the oviduct can be seen as a thin, unconvoluted and almost transparent ribbon extending from the cloaca anteriorly and laterally against the dorsal peritoneum.

The increase in size of the gonads is correlated with an increase in body length as can be seen from Figure 12 in which body length is plotted against maximum follicle size or maximum testis length for juveniles between 20 and 40 mm body length.

During the summer and fall following birth the gonads develop to such an extent that it is frequently difficult to distinguish a mature from an immature individual on the basis of testis or follicle size alone. The vasa deferentia and oviducts are of little additional help because of enlargement of the former and convolution of the latter which obviously occurs well in advance of ovulation. The size of follicles may be as little as 0.1 mm, but most are 0.3 mm and greater and most are less than 1.0 (Fig. 12). It is possible that those females with follicles greater in size than 1.0 mm are old adults.

The Corpus Luteum

The corpus luteum is not often discussed by authors writing on reproduction in lizards, so little information on these structures is

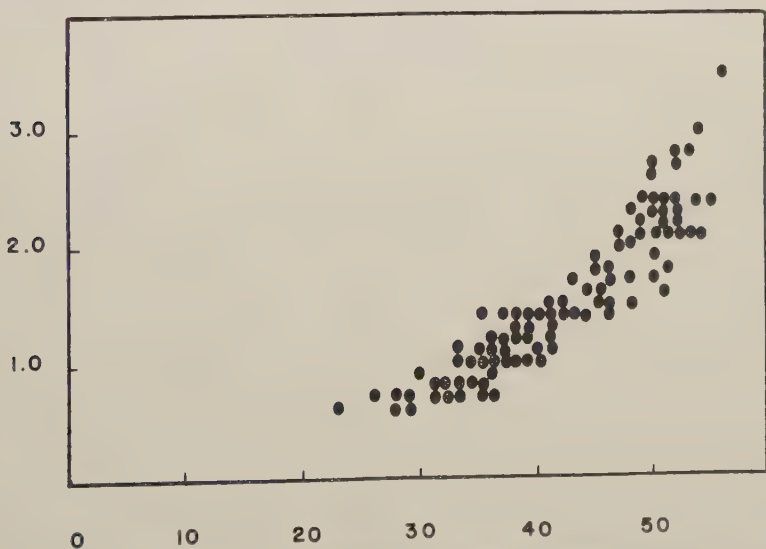


Fig. 11.—Maximum length of testis of *Uta stansburiana* in August to September. Abscissa: body length in mm; ordinate: size of testis in millimeters.

available for most species although some detailed histological studies have been made by several authors including Panigel (1956), Weekes (1934), and Miller (1948). The stages of luteal formation and degeneration described by Weekes (*supra cit.*) are similar to those observed macroscopically in *Uta stansburiana*.

The corpus luteum in *Uta stansburiana* is a large doughnut-shaped structure which rapidly regresses following ovulation. It does remain distinct throughout preovipositional development of the oviducal egg as shown by the fact that in only 5 females with oviducal eggs was I unable to find lutea; these scars were present in 39 females after egg laying had occurred.

Follicular Atresia

Follicular atresia is discussed later in relation to its influence on reproductive potential, but seasonal data are appropriate here. It was anticipated that the greatest atresia would occur in late summer because at that time some follicles begin enlargement but are not ovulated because of changes in whatever factors (day length?) govern reproduction. The total number of atretics for each month from the beginning of follicle enlargement to the end of the reproductive season are shown below:

Month	Number of atretics	Per cent of total
February	3	5
March	1	2
April	7	12
May	17	28
June	10	17
July	8	13
August	14	23
Totals	60	100

The tabular data do not show that atresia is most pronounced in late summer, but the August data do not include 8 females which were noted as having atretic follicles, but in which no counts were made. If each of these had only a single atretic follicle, the August percentage would be higher than that of any other month, but not significantly so.

In large atretic follicles the yolk has a peculiarly granular or flocculent appearance rather than the homogeneous appearance of normal follicles. As the atretic follicle undergoes degeneration it becomes a tiny orange to yellow spot.

Interuterine Migration of Ova

After ovulation, the mature egg passes generally to the oviduct on the same side as the ovary from which it originated. Both Legler (1958) and Tinkle (1959) have commented upon the seemingly high percentage of ovular migration in various reptiles from one ovary to

the contralateral oviduct. Such a transfer is inferred to have occurred when the number of corpora lutea and oviducal eggs on one side or the other are not the same.

Of 135 female *Uta stansburiana* in which accurate counts of both eggs and lutea could be made, interuterine migration occurred in 27 (20%). This compares with a figure of 57 per cent occurrence of migration in the box turtle *Terrapene ornata* (Legler, op. cit.).

This ovular migration was from right side to left in 11 and from left to right in 16. In all but one instance, only one egg was involved. In the lone instance of two eggs, two went to each oviduct, but all four came from the same ovary.

It is possible that ovular migration is actually more frequent for it would not be detected if there was a reciprocal exchange of eggs.

REPRODUCTIVE POTENTIAL

Reproductive potential may be determined on three bases. The two most accurate are counts of the number of corpora lutea or of the number of oviducal eggs. Only rarely is there a difference between the number of corpora lutea and the number of eggs present. Always in such cases there were more lutea than eggs indicating that one or more of a given clutch had already been laid. It is not likely that the excess number of lutea represented some resulting from earlier ovulations because these lutea undergo rapid degeneration after egg deposition (see section on corpus luteum). If there were more lutea than eggs, the count of the former was considered the accurate one. Only

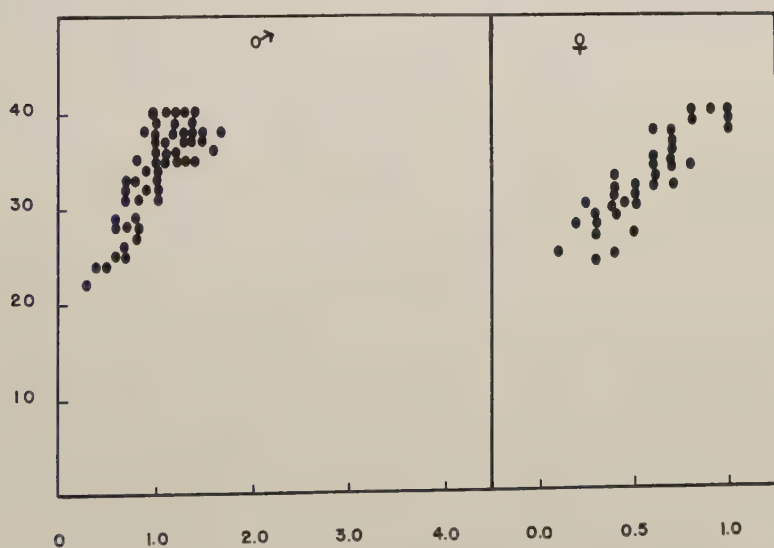


Fig. 12. —Maximum size of testis and of largest ovarian follicles in juvenile *Uta stansburiana* of different sizes. Abscissa: size of testes or of follicles in millimeters; ordinate: body length in mm.

females that were undamaged in capture were used in this part of the study. Follicles and eggs are easily broken in capturing female lizards, making accurate counts difficult or impossible. In some females in which yolk deposition has just begun, it is sometimes difficult to decide which ones will be ovulated and which will not. Therefore, these doubtful individuals were excluded from consideration.

Reproductive potential could be accurately estimated in 363 females containing 1436 eggs, lutea or clearly enlarged follicles, an average of 4.0 per female per clutch. However, as enlarged follicles may not all be ovulated, a comparison was made of potential calculated on the basis of eggs or lutea with that obtained from egg counts. On the basis of enlarged follicles in 194 females, the mean clutch size is 4.2; or the basis of eggs or lutea in 169 females it is 3.9. Most of this difference is attributable to follicular atresia. Follicular atresia is uncommon in *Uta stansburiana* as it was observed in 20 lizards from Winkler County, 21 from Ward County and 7 from Armstrong County, constituting less than 1 per cent of the total number of adults examined. Only 60 atretic follicles were observed in these lizards; in addition, eight females contained an uncounted number, so that the probable total number of atretics seen was about 70 to 75. Thus, possibly 8 to 10 per cent of enlarged follicles undergo atresia.

The reproductive potential on the basis of enlarged follicles was 4.2, on the basis of eggs or lutea it was 3.9. This is a difference of just over 7 per cent. Therefore the decrease can be attributed entirely to atresia. At any rate, both figures (i.e., 4.2 and 3.9) when rounded show an average clutch size of four. Counts of enlarged follicles are accurate for estimates of clutch size. Fitch (1954) in a study of the lizard *Eumeces fasciatus* remarks that counts of enlarged follicles in that species are high compared with counts of oviducal eggs. However, no figures are given in support. He maintains that there are usually small ova of intermediate size between the large ovulatory ones, and the small white ones without yolk. This situation does not exist in *Uta stansburiana* unless counts are attempted during the nonreproductive season before yolk deposition. He also mentions that among the large follicles there may be some that are much smaller than others and which might not become part of the same clutch. This situation does occur in *Uta stansburiana* and occasionally it is difficult to determine objectively which will be ovulated, but this is rarely true.

Reproductive potential in most lizards and in most reptiles varies directly with the size of the female. The lizards were divided into four arbitrary size groups and the mean potential for a female in each group calculated as follows:

Size class (in body length)	Number of females	Mean potential
35-39	4	3.3
40-44	89	3.6
45-49	230	4.0
50-54	40	4.9

It is evident that there is an increase with increase in size with the biggest increase coming in lizards over 50 mm in length.

The mean reproductive potential is only slightly different in the three populations studied. The potential in the northern population is 4.2; in the Winkler County population, 4.2; and in Ward County, 3.6. That this difference is not due entirely to differences in the percentages of size groups in the three populations may be seen from the following tabulation.

Sample area	Size classes and per cent of females in each			
	35-39	40-44	45-49	50-54
Armstrong	3%	39%	55%	3%
Potential	3.3	3.7	4.0	5.7
Winkler	0%	10%	69%	21%
Potential		3.7	4.1	4.8
Ward	1%	31%	64%	5%
Potential	3.0	3.3	3.7	4.6

There do not appear to be any differences in the Armstrong and Winkler County populations despite the difference in size group frequencies except in the size group 50-54 in which the potential of Armstrong County females is almost one egg greater. However, this difference may be one of sampling bias because only a few females of this size are available from Armstrong County (see Fig. 3). The differences between Armstrong County and Ward County are small, but may be important because the potential is greater for every size group in Armstrong County than Ward. It may be that there are selective pressures peculiar to the Ward County population favoring a smaller clutch size. This would not be possible as Lack (1954) has pointed out unless lizards hatching from smaller clutches have a survival advantage over those hatched from larger clutches. That such differences in clutch size may occur in lizards subjected to different competitive situations and that clutch size may be inherited has been demonstrated in a study of the lizard *Lacerta sicula* by Kramer (1946).

The possibility of year to year variation in reproductive potential was also studied. The samples of 1959 were compared with those of 1960. It was unfortunately necessary to omit the Armstrong County data because, although covering a longer period of time, there were not sufficient large samples. The mean potential of Ward County females in 1959 was 3.7, in 1960, 3.5. Comparable figures for Winkler County are 4.6 and 3.9, respectively. Although other explanations for the big change in the Winkler population are possible, the most plausible is a change in frequency of the size classes. The data for 1959 and 1960 do show a decrease in percentages of individuals in the larger size groups as shown below:

		35-44	45-54
Ward County	1959	27%	73%
	1960	34%	66%
	1959	47%	96%
Winkler County	1960	15%	85%

The larger decrease is 11 per cent in Winkler County, but this is not much greater than the 7 per cent decrease in Ward County, so the decrease in potential in Ward County may be completely attributable to this change in percentage, but other factors may be involved in the more significant reduction occurring in Winkler County.

The clutch size may also vary with reproductive season. The average clutch size for the entire reproductive season falls but little from March to June, but does decrease rapidly in July and August. This decrease is doubtless due in part by the last of several clutches in a female containing fewer eggs, but is also due to the fact that some of these late clutches are by females (young of the previous summer) that matured late in the current reproductive season and are producing their first clutch. Although I have not made measurements, it is my impression that the eggs in the small clutches of only two eggs are distinctly larger with more yolk than eggs from larger clutches.

The mean figures for clutch size based on large samples from all populations combined are as follows: March, 4.2; April, 4.2; May, 3.9; June, 3.9; July, 3.1; August, 2.7. These figures indicate that the last clutch of the season is about one egg smaller than the first.

Much of the data in the literature on reproductive potentials of lizards is difficult to compare because usually the number of females examined is small; they frequently come from different parts of the range, are of different sizes and collected at different seasons. The data available on North American species are shown in Table III.

These data show that smaller species generally have smaller clutches and that viviparous forms have fewer embryos than oviparous species in the same genus that are of about the same size. Most of these authors note an increasing clutch size with an increase in body size of the female. Exceptions to this are *Sceloporus merriami* (Chaney and Gordon, 1954) and *Scincella laterale* (Johnson, 1953) in which there seems to be no correlation between body size and clutch size.

Fitch (1956) in a study of the collared lizard (*Crotaphytus collaris*) states (p. 237): "Except for anoles which produce only one egg at a time, iguanids have not been known to produce more than one clutch per season." Fitch reported that one collared lizard observed by him laid two. Some iguanid lizards as shown in Table III certainly lay more than one as does *Uta stansburiana* reported in this paper. The data of Chaney and Gordon (1954) on *Sceloporus merriami* do indicate more than a single clutch in that species, too. It seems more likely that multiple clutches will prove to be typical in iguanid species except in viviparous forms with long periods of intrauterine egg development.

Number of Clutches per Season

It was obvious from this study that females lay more than a single clutch per year because many of them have distinct corpora lutea and

yet have follicles in the process of yolk deposition and enlargement. Unfortunately corpora lutea do not persist for any length of time after egg deposition, and no observations could be made on frequency of laying by individual females, so the probable number of clutches per year must be calculated indirectly.

The length of time from which a majority of females have first begun yolk deposition in the spring (February-March) to the time at which a majority contain oviducal eggs will give a measure of the time required for the development of one clutch. This figure can then be divided into the length of the reproductive season defined as the time from which most individuals show follicle enlargement to the

TABLE III.—Comparison of mean reproductive potential per clutch for 18 North American lizards reported in the literature (the V after name of a species indicates it is viviparous)

Species	Author	Average clutch size	Number of clutches counted	Maximum no. of clutches per season
<i>Cnemidophorus sexlineatus</i>	Fitch (1958)	3.0	112	2
<i>Gerrhonotus m. multicarinatus</i>	Fitch (1935)	11.6	13	—
<i>Gerrhonotus m. webii</i>	Fitch (1935)	12.4	7	—
<i>Gerrhonotus coeruleus shastensis</i> (V)	Fitch (1935)	6.3	15	—
<i>Xantusia vigilis</i> (V)	Miller (1951)	1.8	78	1
<i>Eumeces fasciatus</i>	Cagle (1940)	9.2	25	—
<i>Eumeces fasciatus</i>	Fitch (1954)	9.1	182	—
<i>Eumeces obsoletus</i>	Fitch (1955)	11.4	13	—
<i>Eumeces septentrionalis</i>	Breckenridge (1943)	8.8	19	—
<i>Scincella laterale</i>	Johnson (1953)	3.3	31	2
<i>Anolis carolinensis</i>	Gordon (1956)	1.0	—	6-9
<i>Dipsosaurus dorsalis</i>	Norris (1953)	3-8	—	—
<i>Holbrookia texana</i>	Cagle (1950)	6.6	14	Several
		June-July		
		3-6	10	—
		August		
<i>Crotaphytus collaris</i>	Fitch (1956)	7.6	29	2
<i>Sceloporus merriami</i>	Chaney and Gordon (1954)	3.7	27	1?
<i>Sceloporus undulatus</i>	Crenshaw (1955)	7.6	11	Possibly more than 1
<i>Sceloporus olivaceus</i>	Blair (1960)	11.3 yearlings	—	4 except yearlings
		18.4		
		2-year		
		24.5		
		3-year		
<i>Sceloporus cyanogenys</i> (V)	Hunsaker (1959)	12.6	7	—

time at which most individuals have ceased laying. The data presented are for Ward and Winkler county populations only.

In 1959, the majority of females had follicles just beginning enlargement on February 13, while in 1960 the majority had not begun enlargement until March 10. In 1959, most females had oviducal eggs on March 22; in 1960, on April 16. Thus, the time for the development of the first clutch was 38 days in 1959, 37 in 1960.

The length of the reproductive season was 141 days in 1959 and 121 days in 1960. Dividing these figures, respectively, by 3.8 and 3.7 gives 3.7 and 3.3 for the number of clutches.

It may be argued that the development of the clutches after the first will proceed more rapidly because of higher temperatures and a longer activity period. However, I think that any one female laying more than 3 clutches is unlikely because the figures obtained allow no time for oviducal retention of the eggs which must be at least one week, but probably longer. Too, the reproductive season for any single female will probably not be as long as the figure above because females maturing late in their second season will reproduce late and thus extend the reproductive season of the population beyond what it would be for an individual.

By multiplying an average figure of three clutches per year by the mean potential for each female, an average annual potential per female for each population would be as follows: Ward, 10.8; Winkler, 12.6; Palo Duro, 12.6 if three clutches per year is also normal there, but data are insufficient to be certain of this.

On the same basis, the proportion of the potential contributed by each size class can be calculated as shown below:

Size classes (mm)	Armstrong County	Winkler County	Ward County
35-39	9.9	—	9.0
40-44	11.1	11.1	9.9
45-49	12.0	12.3	11.1
50-54	17.1	14.4	13.8

By having the percentage of females of each size class in a given population at the beginning of the reproductive season would make possible the calculation of the number of eggs laid in a given population. Such an estimation was attempted in the summer of 1960 in the Winkler population in a 10,000 square yard area. All females in the population were marked. Of the total number of adults marked 18 had their home ranges, based on at least 3 captures, largely confined to the study area or immediate margin. The size distribution of these females is as follows and the potential number of eggs is:

40-44 mm — 1	11
45-49 mm — 14	172
50-54 mm — 3	43

Total 226

The total number of hatchlings potentially produced was 226. The total number of hatchlings marked in the same area was 174. The juveniles have exceptionally strong homing tendencies, so little emigration or immigration occurred making the above figures more reliable. Although 174 young were marked in the area, unmarked young still were present on the last trip in late October showing that the actual number was greater than 174.

Relation of Potential to Total Number of Ovarian Follicles

Counts were made in some females of all macroscopically visible follicles to determine if such counts, for example during the winter, were useful in estimating reproductive potential for the following year. Counts were also made in juveniles and in adults at all seasons. It was also hoped that counts of total numbers might indicate number of clutches deposited. The data are shown in Table IV.

The total number of ovarian follicles at any season will not give an accurate estimate of reproductive potential. The average number of follicles present in adult females during the winter is about the same as in prereproductive females during January to March and both these counts are about the same as the counts made just prior to first ovulation, so these three groups could be combined for comparative purposes. It can be seen that there is a slight decrease in the mean of all size groups between that just prior to ovulation with that just afterward. The average decrease for all size groups is from

TABLE IV.—Total number of follicles in female *Uta stansburiana* of different size groups at different seasons and during different stages of the reproductive cycle (all figures shown are means except those in parentheses which are number of specimens)

Period	35-39 mm	40-44 mm	45-49 mm	50-54 mm
Jan., Feb., March (Prereproductive)	17.0(5) Mean of all groups 17.4	17.4(26)	17.5(26)	17.5(2)
July, Aug., Sept. (Post reproductive)	— Mean of all groups 15.9	15.0(2)	16.1(12)	—
October-December (winter)	15.0(1) Mean of all groups 16.8	15.6(8)	18.0(7)	18.0(2)
Just prior to ovulation	16.0(1) Mean of all groups 18.8	18.3(12)	18.3(30)	22.8(6)
After ovulation while oviducal eggs still present	13.0(1) Mean of all groups 16.5	16.4(8)	16.5(47)	18.0(1)
After egg deposition, but prior to new follicle enlargement	— Mean of all groups 19.6	20.7(7)	19.2(22)	—

18.8 to 16.5, a drop of 2.3. If it were assumed that no new follicles appeared just after ovulation this figure of 2.3 could be used as one measure of average clutch size. However, counts of corpora lutea and eggs were also made in those females in which total number of follicles was counted. The actual average clutch size of these females was 3.8.

Ovulation seems to stimulate follicle development. The average number of follicles is greater after ovulation and subsequent egg deposition than at any other time.

The average number of follicles in young lizards was 12.7. From this low, the mean number tends to increase with an increase in body size as can be seen in Table IV. Other than follicles with yolk, no other size group will give an accurate estimate of potential nor are counts of total number of follicles suitable for that purpose.

CONCLUSIONS

Populations of *Uta stansburiana* within 300 miles of one another and belonging to the same subspecies (*stejnegeri*) may differ from one another in several biological attributes.

The sex ratio is little different from 50:50 in any of the three populations regardless of age group or season.

The ratio of juveniles to adults is different from one population to another at different seasons, but data indicate that in all populations over 90 per cent of the individuals are mature during the reproductive season at an age of one year or less.

There is an annual turnover of most of each population. This fact cannot be established satisfactorily from mass samples, but could be from study of marked animals in a study population.

Females reach maturity at a smaller size than males and generally do not grow to the large size of the males. Size at maturity varies between the three populations. The smallest mature individual was 38 mm, the largest individual recorded, 60 mm.

A comparison of age at maturity of North American lizards indicates the iguanid lizards mature faster than scincids regardless of size of the species. Age at maturity may vary geographically.

The maximum size of ovarian follicles in a nonreproductive female is 1.7 mm. These begin enlargement and yolk deposition in February and March and approximately 38 days are required before these follicles will be ovulated at a size of 7 to 8 mm. The initiation of ovarian development in the spring is greatly affected by weather conditions prevailing at this time.

Testis enlargement takes place simultaneously with follicle enlargement until June and July when the testes and vasa deferentia undergo regression.

Oviducal eggs first appear in March and April and for the last time in August.

After ovulation, the corpus luteum formed generally remains distinct until after egg deposition. As long as oviducal eggs are present no ovarian follicles begin enlargement or yolk deposition, but this

process does begin after deposition and sometimes when corpora lutea are still evident.

The gonads of juvenile lizards are very small at birth, but follicles and oviduct are usually differentiated even then, so the sexes are usually easily distinguished. The increase in size of follicles and of the testis is correlated directly with increased body length.

During development of yolked follicles some of these will undergo atresia, but this is uncommon and does not exceed 10 per cent in all adult females examined.

Following ovulation, one egg (in one case two) may be transferred from the ovary to the contralateral oviduct. This occurred in 20 per cent of the females examined. Comparative percentages in other reptiles are presented.

Reproductive potential can be calculated accurately on the basis of the number of enlarged yolked follicles, the number of corpora lutea, or the number of oviducal eggs. Little difference exists in estimates on any of these bases. Counts or measurements of follicles in nonreproductive females cannot be used for estimating potential.

Reproductive potential is lower in smaller lizards, lower late in the season, and in one population compared with the other. Year to year variations are also evident and generally correlated with the percentages of each size group of lizards in the population.

A comparison of reproductive potential in North American lizards shows that it is lower in viviparous forms, in smaller species, and in scincid as opposed to iguanid lizards.

Uta stansburiana probably lays three clutches of eggs per year. Multiple clutches seem to be characteristic of many North American lizards.

A study of the total reproductive potential of a lizard population was made by knowing the number of females present in a study area and their sizes. The figure for their potential egg production (226) was very close to the actual number of hatchlings marked in the study area (174).

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Variation in Populations of Brown Snakes, Genus *Storeria*, Bordering the Gulf of Mexico

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ABSTRACT: Examination of specimens of *Storeria* from coastal areas of Louisiana and Texas indicates the existence of a distinctive population inhabiting the coastal marshes. On the basis of color pattern and scutellation this population is sharply distinct from populations of *Storeria dekayi* on adjacent higher ground and appears closely allied to *Storeria* of Mexico, Guatemala and Honduras. The few specimens suggesting possible interbreeding with contiguous high ground populations come from areas of ecological disturbance and appear to represent occasional hybridization, rather than an indication of intergradation.

Specimens believed by Trapido to represent intergrades between *Storeria dekayi temporalineata* and *S. d. texana* or *S. d. wrightorum* were derived from the distinctive marsh population, and the southern and northern groups of subspecies placed by Trapido in the species *Storeria dekayi* thus appear to be reproductively isolated. *Storeria tropica* Cope is therefore revived for the southern group, with four subspecies; *Storeria tropica tropica*, *Storeria tropica anomala*, *Storeria tropica temporalineata*, and *Storeria tropica limnetes*, subsp. nova, the population of the Louisiana and Texas coastal marshes.

In his monograph of the snakes of the genus *Storeria*, Trapido (1944) recognized six subspecies of *Storeria dekayi*, distributed from the northeastern United States to Guatemala and Honduras. Three of these subspecies, *S. d. texana*, *S. d. wrightorum*, and *S. d. dekayi* occur north of the Rio Grande and replace each other from west to east, between the Great Plains and the Atlantic Coast. As defined by Trapido, the easternmost subspecies, *dekayi*, is found from the Atlantic Seaboard to the western side of the Appalachians. Its northern limit is the limit of the species distribution in Quebec and it intergrades with *S. d. wrightorum* over a broad area extending from the Carolinas around the southern Appalachians and northward to Illinois. Subspecies *wrightorum* extends from this zone of intergradation westward across the Mississippi valley and intergrades with *S. d. texana* along a line from Iowa to western Louisiana. Subspecies *texana* is found between this line and the eastern edge of the Great Plains and extends southward to the gulf coast of Texas and into Mexico as far south as Hidalgo.

The three remaining subspecies which Trapido recognized are found in Mexico, Guatemala and Honduras. They are described as replacing each other southward along the gulf coastal plain, with *S. d. temporalineata* extending from the Rio Grande south into Veracruz, where *S. d. anomala* occurs. The latter is said to be characteristic of an area about the towns of Orizaba and Jalapa. It presumably intergrades with *S. d. tropica*, which inhabits the Atlantic drainages of Guatemala and Honduras.

The three southern subspecies were based on a small number of specimens and their relationships and distributions are not clearly established in Trapido's monograph. In the northern group, where material was much more abundant, the three subspecies are represented as intergrading over relatively broad strips along their mutual boundaries (*S. d. dekayi* x *S. d. wrightorum* and *S. d. wrightorum* x *S. d. texana*). In contrast to these broad zones of intergradation Trapido indicated, without comment, a very peculiar pattern of intergradation between the southern group, represented here by *S. d. temporalineata*, and the northern group represented by *texana* and *wrightorum*. Subspecies *temporalineata*, as was indicated above, was said to reach the northernmost limit of its range at the Rio Grande. In his discussion of this subspecies, however, Trapido noted that specimens showing its characteristics had been collected as far to the northeast as Mississippi. He designated these specimens, some 20 in number, as intergrades between *temporalineata* and one or the other of the two northern subspecies occurring in this region. With one exception, a specimen from Natchitoches Parish, Louisiana,¹ the supposed intergrades were restricted to a narrow strip immediately adjacent to the coast, implying an area of intergradation some 700 miles long, and generally less than 20 miles wide. Such a column-like intergradation pattern would seem to require an explanation. In the words of Schmidt (1953) it is, "not geographically intelligible."

The localities from which the presumed intergrades were taken, with the aforementioned exception, are in or at the edge of the great coastal marshes of Louisiana and east Texas. Trapido's data thus suggest that a distinctive marsh population exists in this area, rather than a tenuous and peculiarly penetrating kind of intergradation. In 1949 the growth of the Tulane University Collections had led to the accumulation of a sufficient number of specimens of *Storeria* from the Louisiana marshes to confirm the existence of such a population and to make an analysis of its relationships possible. Studies upon which this report is based were begun at that time at the suggestion of Dr. Fred R. Cagle of Tulane and have been pursued intermittently since. The author wishes to express his gratitude to Dr. Cagle for encouragement in the initial phases of the study and to Mrs. Emily Reid, staff artist of the Department of Zoology, University of California, Berkeley, for final preparation of the figures.

MATERIALS AND METHODS

One hundred and eighty-seven *Storeria* from Mississippi, Louisiana, and Texas; the Mexican states of San Luis Potosi, Nuevo

¹ This specimen, CU7364, from Chastine, La. is in poor condition with markings somewhat obscured, but appears to be typical of *S. d. wrightorum* in all features. The locality listed by Trapido, Creston, is apparently an error.

Leon, Veracruz and Puebla; Guatemala and Honduras, have been examined.

The author is indebted to the following institutions and individuals for opportunity to examine specimens. The abbreviations to be used subsequently are shown in parentheses: Dr. Fred R. Cagle, Tulane University (TU); Dr. Richard G. Zweifel, American Museum of Natural History (AMNH); Dr. Arthur Loveridge, Museum of Comparative Zoology, Harvard University (MCZ); Dr. Doris M. Cochran, United States National Museum (USNM); the late Karl P. Schmidt, Chicago Natural History Museum (CNHM); Dr. Norman Hartweg, University of Michigan Museum of Zoology (UMMZ); Dr. William J. Hamilton, Jr., Cornell University (CU); Dr. E. Raymond Hall, Museum of Natural History, University of Kansas (KU); Dr. Bryce C. Brown, Baylor University (BU or BCB); Dr. Robert C. Stebbins, Museum of Vertebrate Zoology, University of California (MVZ); Mr. Richard E. Etheridge, Department of Zoology, University of Michigan (REE), and Mr. Roger Conant of the Philadelphia Zoological Garden for aid in obtaining material from the collections of the Academy of Natural Sciences of Philadelphia.

Color pattern, body proportions, size, and the number of ventral and subcaudal scales were the basis for analysis of geographic variation. Data recorded for each specimen examined were as follows: sex; snout-vent length; tail length; number of ventral scales, beginning with the first unpaired scale between the chin shields and not including the divided anal; number of subcaudal scales, beginning with the first scale to reach the midline behind the vent and including the conical scale at the tail tip; upper and lower labials. Head markings were recorded on a mimeographed diagram of the head in lateral view. Written descriptions of the markings of the upper and lower labials and the anterior temporal as seen on the left side, or on the right if the left side of the head was damaged, supplemented the diagrams.

PATTERNS OF VARIATION

The populations originally described by Trapido were distinguished primarily on the basis of differences in scutellation and color pattern. In respect to the latter, the six subspecies fall into two distinct groups. The northern group is characterized by the presence of dark markings on the upper labial scales and by the presence of a vertical dark bar across the anterior temporal (*S. d. dekayi* and *S. d. wrightorum*), or by an anterior temporal with only a narrow dorsal edging of dark pigment (*S. d. texana*). The southern group (*S. d. temporalineata*, *S. d. anomala* and *S. d. tropica*) is characterized by the absence or near absence of labial markings, and by the presence of a fine median horizontal dark line on the anterior temporal scale. Superficial examination may permit confusion between this line and the dark dorsal edging commonly found on this scale in *S. d. texana*, but careful observation shows these two patterns to be distinct.

In counts of ventral and subcaudal scales, numbers are lowest in specimens from the northeast and increase to the southwest in

the northern group of subspecies. In the southern group the counts are characteristically slightly higher, but there is a considerable overlap with the highest of the counts found in *S. d. texana* from Mexico.

In attempting to ascertain the status of the population of the coastal marshes the most critical indication of relationship would appear to lie in color pattern. In respect to the marking of temporal and labial scales referred to above this population falls clearly with the southern group and without exception specimens from the marshes of the Mississippi delta and the coast to the westward conform to the color pattern characteristic of Trapido's Latin American subspecies. The recording of individual head markings on standard diagrams provides a basis for demonstration of the distribution of the different color patterns and the distinctions between them as shown in Figure 1. Composite diagrams representing the aggregate of head markings of all individuals in samples from selected localities are shown. The composite diagrams were prepared from individual records by filling in all the markings shown in each series of specimens on a single tracing-paper overlay. Since this technique sums all the head markings to be found in a sample, it tends to emphasize any similarity which exists between adjacent populations by giving a single intermediate individual as much weight as a large number of identical and divergent ones. Despite this bias the distinctness of the marsh populations from the contiguous populations on higher ground and the affinity of the former to the southern group of subspecies are clearly shown in the figure. Comparison of the mid-temporal line as found in southern and marsh populations may be made with the dorsal dark edging shown in populations of *S. d. texana* represented by diagrams A and B.

Additional points may be made with reference to Figure 1. On the southern Texas coast the marshes disappear but a series of off-shore bars does occur. Few specimens are available from this area, but those which have been examined support the conclusion that this strip of arid coast isolates the marsh populations from those of similar color pattern to the south. The coastal islands are apparently inhabited by populations typical of subspecies *texana* (e. g. the specimens from St. Josephs Island represented by diagram "A". These specimens, eleven in number, are a single adult female and her 10 young — UMMZ 72355 A-K). A second point is that Figure 1 suggests a useful diagnostic character overlooked by Trapido. While there is considerable variation in the markings of the temporal scale, and of the upper labials in general, the three northern subspecies are consistent in the presence of dark pigment on the most posterior scales of both the upper and lower labial series, whereas the marsh and southern populations are equally consistent in lacking such a dark marking at the corners of the mouth.

A final point to be made in reference to the figure is that *Storeria dekayi victa* (diagram "E" is taken from Trapido's plate) shares this characteristic (absence of a spot at the corner of the mouth) with the coastal populations which are the subject of the present paper

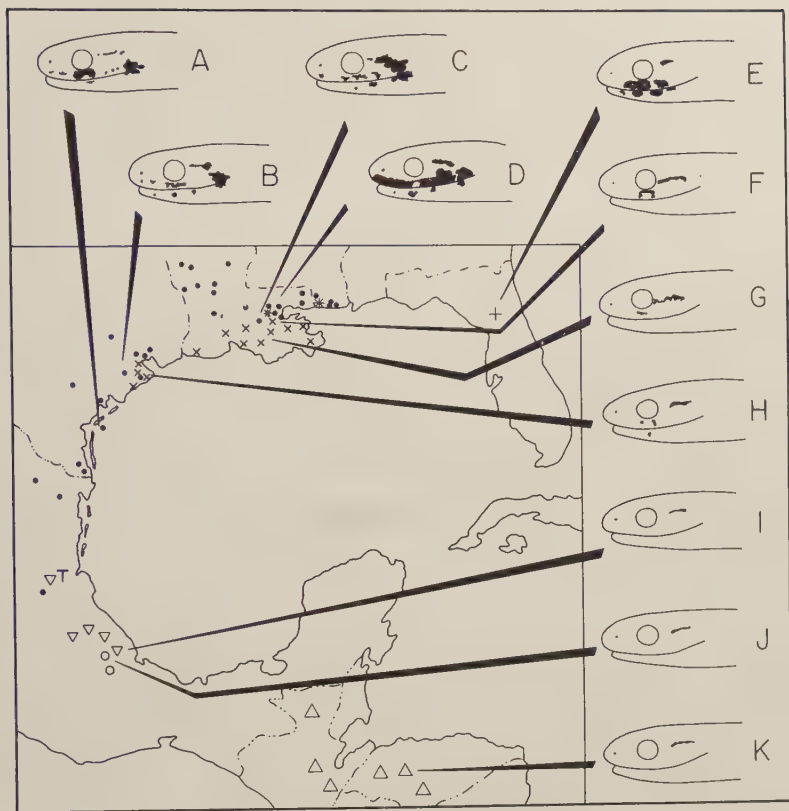


Fig. 1.—Localities from which specimens were examined and head markings in selected populations. Taxonomic assignment of the specimens is indicated as follows: *Storeria dekayi*—solid circles; *Storeria tropica limnetes*—crosses; apparent hybrids between *S. dekayi* and *S. t. limnetes*—asterisks; *Storeria tropica temporalineata*—inverted triangles; *Storeria tropica anomala*—open circles; *Storeria tropica tropica*—erect triangles. The northernmost record for *S. t. temporalineata*, indicated by the superscript^T, is based on Trapido (1944). The specimen was not seen by the present author. The diagrams of head markings are composites of all markings in a particular sample as follows: A—10 specimens from St. Joseph's Island, Texas; B—4 specimens from Harris and Brazoria counties, Texas; C—13 specimens from New Orleans, La.; D—6 specimens from Livingston and St. John the Baptist Parish, La.; E—1 specimen of *Storeria dekayi victa*, Alachua County, Florida, the diagram taken from Trapido's illustration (Trapido, 1944, p. 40); F—4 specimens from Orleans and Jefferson parishes, La.; G—4 specimens from Terrebonne and LaFourch parishes, La.; H—4 specimens from Harris and Brazoria counties, Texas; I—2 specimens of *Storeria tropica temporalineata* from the State of Veracruz, Mexico; J—1 specimen of *Storeria tropica anomala* from the State of Veracruz, Mexico; K—3 specimens of *Storeria tropica tropica* from the Subirana Valley, Honduras.

and this fact should probably be taken into account along with the observations of Neill (1950) in a reconsideration of its relationships.

Further analysis of the color pattern affinities of the marsh population may be carried out by concentrating attention on the total number of upper labials on which any black pigment occurs. The histograms in Figure 2 show that of 53 specimens from the marshes, 50 have 3 or fewer labials with such pigment (94%), while 96 of

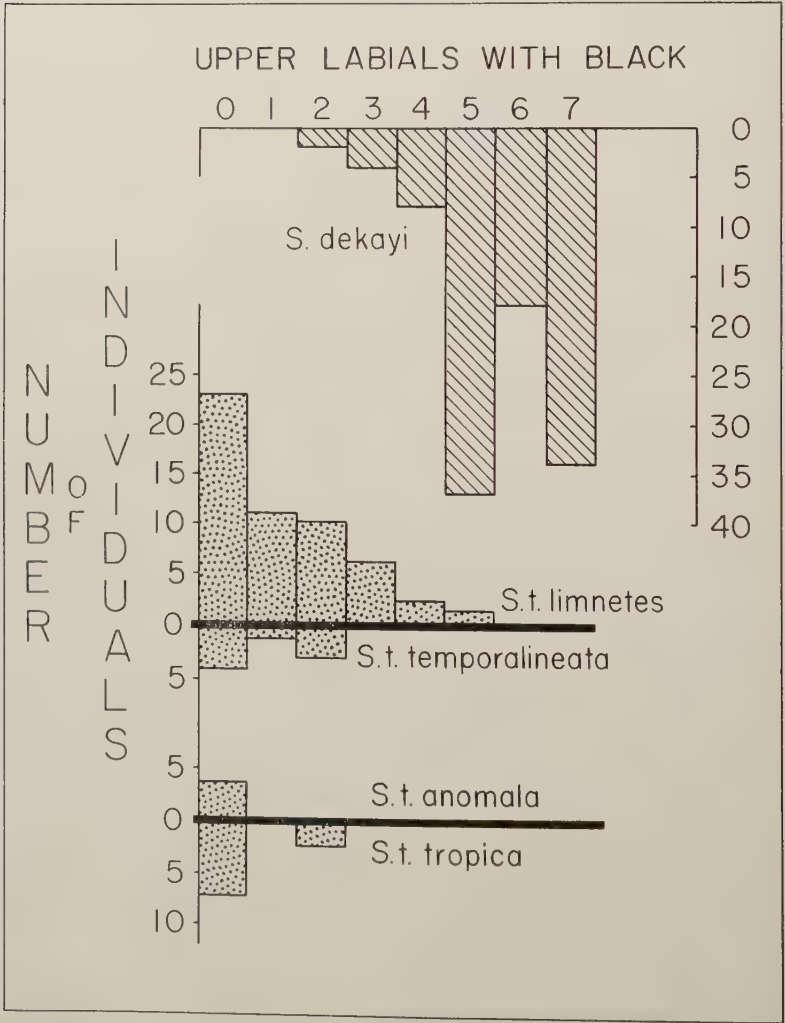


Fig. 2.—Frequency histograms showing the number of upper labials bearing dark markings in the samples of *Storeria dekayi* and *Storeria tropica* examined. Vertical scales indicate the number of individuals.

101 specimens from adjacent higher ground (95%) have 4 or more labials with dark pigment.

An analysis of the body proportions, as indicated by the ratio of total length divided by tail length, showed no significant differences

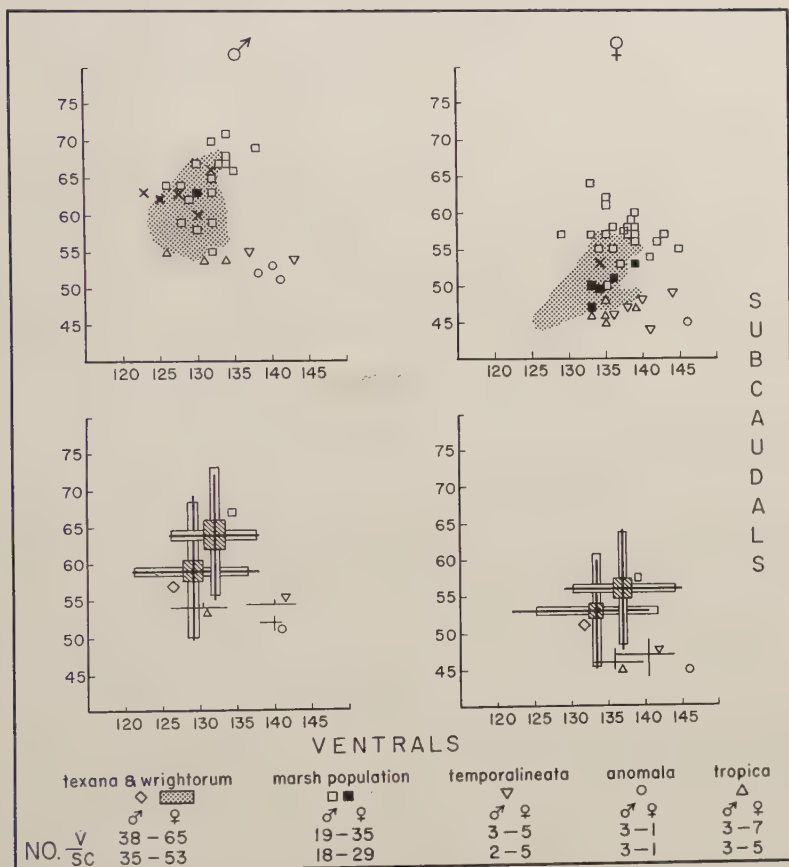


Fig. 3.—Scatter diagrams and modified Dice-Leraas graphs showing counts of ventral and subcaudal scales. The Dice-Leraas graphs show two standard deviations and two standard errors on either side of the means, which are indicated by the junctions of the lines indicating the range. Ranges and means only are indicated for southern populations of *Storeria tropica*. The shaded area, used in the interest of clarity to indicate the scatter of counts for *Storeria dekayi*, shows the area of concentration of scatter points only. Six extreme males and six extreme females of this species fall outside the shaded area. These are included in the Dice-Leraas graphs and in the totals of specimens indicated across the bottom of the figure. Solid squares indicate specimens of *S. t. limnetes* from Cameron Parish, La., and from Texas. Specimens intermediate in color pattern between *S. t. limnetes* and *S. dekayi* are indicated by crosses.

between marsh and high ground populations. With respect to size, comparison of total lengths supports an impression that snakes from the marshes average larger. Total length of 16 adult males and 27 adult females from the marsh population in Louisiana ranged respectively from 215 to 384 mm and 219 to 411 mm with means of 293 and 320 mm. In the high ground populations from Louisiana 22 males varied from 183 to 326 mm with a mean of 261 and 30 females varied from 186 to 405 mm with a mean of 285. Thus, in the Louisiana populations marsh animals average about 12 per cent longer.

Analysis of ventral and subcaudal counts is carried out in Figure 3 using scatter diagrams and modified Dice-Leraas graphs. In the scatter diagrams the marsh specimens, represented by squares, tend to have higher counts of both subcaudal and ventral scales than do specimens from the adjacent populations of *S. d. wrightorum*, *S. d. texana* and their intergrades (stippled area) taken from the adjacent higher ground. Moreover, the marsh populations are not intermediate with respect to subcaudal scales, but instead represent the extreme. Surprisingly the marsh population is most sharply separated from the populations to the south which share the same color pattern. Specimens from Harris and Brazoria Counties, Texas, are represented by the solid squares and show a tendency to be intermediate between those from the marshes to the north and specimens designated as *S. d. temporalineata* from Mexico. The Dice-Leraas graphs indicate that the differences between marsh and high ground populations are statistically significant though not to the extent usually accepted as a basis for taxonomic distinction.

Referring once more to Figure 1 and noting the localities from which the specimens referred to were taken, it is clear that a distinctive form of *Storeria* inhabits the coastal marshes of Louisiana and Texas. The taxonomic status of this population hinges upon its relationships to the southern and northern subspecies groups, and, conversely, the relations of these groups to each other depends upon the status of the marsh population. On the basis of color pattern the *Storeria* of the marshes seems clearly to be a representative of the southern group, while on the basis of scutellation it is distinct from the same southern populations on a level which can best be indicated by subspecific recognition. The critical question is that of intergradation between the marsh population and populations representing the northern group of subspecies.

Sympatry of the marsh and high ground forms has been observed along the Mississippi River levees in and near New Orleans where they may occasionally be taken under the same bit of cover. Specimens characteristic of both forms have also been examined from Jackson Lake, Brazoria County, Texas. Since the marsh population occupies such a narrow strip, the massive zones of intergradation found between the subspecies which comprise the northern group are not possible and it might appear that the very narrowness of the range of the marsh population argues against the existence of

any extensive gene exchange with the high ground populations. However, the Gulf Salt Marsh Snake, *Natrix sipedon clarki*, occupies the same marshes and maintains its identity while interbreeding with freshwater forms (*N. s. confluens* and *N. s. fasciata*) so it should be assumed that selective forces can maintain subspecific differences in the area with which we are concerned.

Since scale counts overlap so broadly, evidence of intergradation must be sought primarily on the basis of intermediacy of color pattern. Three criteria might aid in recognition of possible intergrades: presence of both a temporal line and dark pigment on the 7th upper and lower labials, reduction in size or absence of the dark mark at the corner of the mouth, or a temporal marking intermediate between the horizontal line and the diagonal bar. Scale counts of individuals having such color patterns might be expected to fall in the zone of overlap. Among 164 specimens examined from the marsh population and from the populations of *S. d. texana* and *S. d. wrightorum* peripheral to the marshes, 6 specimens have been found which show some of these features. Two of these (TU 14255 and TU 14256) are intermediate in color pattern but have ventral scale counts below the extreme range of the marsh population (123 and 125, respectively). A third specimen (TU 14265) from the same locality as the two referred to above has the 7th labials unmarked, a high ventral count, and a heavy horizontal dark bar on the dorsal third of the temporal. These specimens come from Hancock Co., Mississippi, at the eastern terminus of the marshes. A specimen from nearby Biloxi, Mississippi, and two from New Orleans (UM 76821, TU 12163, USNM 12923) are similarly intermediate in both scale counts and color pattern. Feuer (1959) has reported a single brood from New Orleans in which some individuals exhibited horizontal and others diagonal bars on the temporal scale. It is the opinion of this investigator that the number and distribution of these intermediate specimens suggests local hybridization rather than the existence of true intergradation. The areas from which the intermediate specimens come have been subject to extensive ecological disturbance as the result of human activities and the relationship between *Storeria dekayi* and *Storeria tropica* may be another example in the growing list of species which undergo some degree of breakdown of reproductive isolation under such conditions. In the New Orleans area specifically, this has been demonstrated in the case of two other species with somewhat similar distributions. Volpe (1960) has reported the common occurrence of hybrids between the toads *Bufo valliceps* and *Bufo fowleri* despite the apparent sterility of all viable hybrids. Evidence of populations of *Storeria* of an intermediate nature existing anywhere along the great extent of ecotone between marsh and higher ground is lacking and it appears that the marsh population is reproductively isolated from *S. d. texana* and *S. d. wrightorum*. This conclusion splits the northern and southern groups of subspecies and necessitates the revival of Cope's name, *Storeria tropica*, for the southern group (Cope, 1885). The marsh population studied here belongs

to the *tropica* group, but is subspecifically distinct from the previously described forms on the basis of the high subcaudal counts and is recognized as a new subspecies under the name *Storeria tropica limnetes* [limnetes, meaning "living in marshes," (Woods, 1944)]. The three subspecies described by Trapido from Mexico, Guatemala, and Honduras were described on the basis of insufficient material and may not all be valid, but adequate numbers of specimens are still not available for a reconsideration of their status at this time. They are therefore retained as subspecies of *Storeria tropica*.

Storeria tropica Cope
Tropical Brown Snakes

Storeria tropica Cope, Proc. Amer. Philos. Soc., vol. 22, p. 175, 1885.
Storeria dekayi tropica Trapido, Amer. Midl. Nat., vol. 31, no. 1, p. 77, 1944.

Holotype.—USNM 6759, collected at Peten, Guatemala, by H. Hague.

Diagnosis.—Distinguished from *Storeria dekayi* by: (1) the absence of dark markings at the corners of the mouth, on the rearmost upper and lower labials; (2) the presence of a horizontal dark line through the long axis of the anterior temporal scale.

Discussion.—*Storeria tropica* as first described by Cope (1885) was considered to be distinct on the basis of the temporal line and the presence of only six supra-labials, rather than the seven characteristic of *Storeria dekayi*. The material now available shows the latter character not to be diagnostic. Labial counts show variation in both species and appear to be particularly variable in the Honduran and Guatemalan populations of *Storeria tropica*. Labial counts range from five to eight in the specimens which are available from this region.

Storeria tropica tropica Cope
Tropical Brown Snake

Storeria tropica Cope, Proc. Amer. Philos. Soc., vol. 22, p. 175, 1885.
Storeria dekayi tropica Trapido, Amer. Mid. Nat., vol. 31, no. 1, p. 77, 1944.

Holotype.—USNM 6759, collected at Peten, Guatemala by H. Hague.

Diagnosis.—This population was distinguished from *Storeria temporalineata* by Trapido on the basis of a lower number of ventral plus subcaudal scales and a "reduced, more pointed snout." With respect to scale counts this diagnosis is slightly misleading since specimens from the range of *S. t. tropica* and from Mexico suggest that the populations represented are identical in subcaudal counts and that the difference in the total count is the result of a tendency toward a lower number of ventral scales in *S. t. tropica*. This subspecies is distinguished from *S. t. anomala* in that it has only two pairs of



Fig. 4.—*Storeria tropica limnetes* Holotype, TU 11374.

chin shields and from *S. t. limnetes* by lower counts of subcaudal scales.

Specimens examined.—USNM 35921, USNM 6759, MCZ 387146, MCZ 49989, CNHM 20527, CNHM 21796, CNHM 411, AMNH 70208.

Storeria tropica anomala (Dugés)

Orizaba Brown Snake

Storeria dekayi var. *anomala* Dugés, Proc. U.S. Nat. Mus., vol. 11, pp. 9-10, figs., 1888.

Holotype.—Reportedly in Mus. Alfredo Dugés, Univ. Guanajuato, Mexico (Trapido, 1944, Smith and Taylor, 1945).

Diagnosis.—Differs from all other subspecies of *Storeria tropica* in the presence of three pairs of chin shields, rather than two.

Specimens examined.—USNM 5565, USNM 7081, USNM 8939, USNM 110328.

Storeria tropica temporalineata (Trapido) New comb.

Mexican Brown Snake

Storeria dekayi temporalineata Trapido, Amer. Mid. Nat., vol. 31, no. 1, p. 70, 1944.

Holotype.—USNM 32148, collected at San Rafael, Jicaltepec, Veracruz, Mexico by C. H. Thompson.

Diagnosis.—Differs from *Storeria tropica tropica* in having a larger number of ventral scales and from *Storeria tropica limnetes* in having a lower number of subcaudal scales. Distinguished from *Storeria tropica anomala* by the presence of only two pairs of chin shields.

Specimens examined.—USNM 32148, USNM 52300, MCZ 15990, MCZ 2843, UMMZ 99541, UM 85966, KU 23906, AMNH 4292.

***Storeria tropica limnetes* subsp. nov.**

Marsh Brown Snake

Fig. 4

Holotype.—Tulane University Collections 11374, a male collected by Horace Whitten at Waggaman, a settlement south of Harahan, St. Charles Parish, Louisiana on December 2, 1944.

Diagnosis.—Distinct from all other subspecies of *Storeria tropica* in the higher number of subcaudal scales. Differs from *Storeria tropica anomala* in that it has only two pairs of chin shields.

Description of Holotype.—(Fig. 4) Adult male; total length 311 mm, tail length 74 mm; scale rows on body 17 - 17 - 17, ventral scales 134, subcaudals 71, supralabials 7-7, infralabials 7-7, postoculars 2-2, posterior temporals 2-3, chin shields—2 pairs. Coloration: (in alcohol) Ground color of dorsum Pearl Grey (Maerz and Paul 1950, A-1 in plate 44, page 110), venter Oyster White (Maerz and Paul 1950, B-1 in plate 10, page 43). The dorsal ground color extends over the lateral portions of the ventral scutes so that each has a more or less triangular darker portion on either end where it interdigitates between the dorsal scales of the lowermost row. On the head only the postnasals and 2nd, 5th, 6th and 7th supralabials are immaculate. The 1st supralabials each have a single small dark fleck, while the 3rd and 4th have irregular vertical bars near and parallel to their posterior margins. The internasals, prefrontals, frontal, preoculars, postoculars and parietals all are peppered with dark flecks, increasing in number posteriorly. On the parietals these flecks fuse to form a stripe paralleling the posterolateral edge of each scale. At the junction of the two postoculars there is a fusion of dark flecks to form a blotch behind the eye which is in line with, but not continuous with, the temporal stripe. The temporal line is an irregular black horizontal stripe slightly above the midline of the scale. This line does not quite reach the margin of the scale at either end. On one side both posterior temporals have scattered flecks while on the other side only the dorsal one is so marked. The infralabials and chin shields are immaculate.

A pair of elongate dark spots form an open-ended "V," centered on the dorsal midline of the neck with the wide opening anterior-most. Posterior to this mark there begins a series of paired dark dorsal spots. These tend to fuse to form bars, but only three such bars are complete. The complete bars are located about 1/3 of the body length behind the head. Posterior to this region the spots become smaller and a partially defined lighter median dorsal stripe appears. On the tail, dorsal dark spots are small and mostly confined to the anterior third. Anteriorly, the ventral scales each have 2 to 4 fine dark flecks. These become finer and fewer posteriorly and most of the subcaudals are immaculate. Hemipenis: Terminally there is a crescent-shaped spine-free area. Spines adjacent to this are relatively small. Progressing toward the base the spines become slightly larger. About

1/3 of the way from the base is a zone of large spines. The largest are a pair located dorso-medially and a pair located dorso-laterally. Ventrally there are about 9 definitely enlarged spines in this zone.

Variation.—As was indicated previously, specimens from east Texas have lower subcaudal counts and thus tend to approach *S. t. temporalineata*. In respect to coloration, Trapido's (1944) statement that *temporalineata*-like specimens (those which he designated as intergrades between *temporalineata* and *S. d. texana* and *S. d. wrightorum*) could be recognized by a higher incidence of black markings on the supralabials as compared with specimens of *temporalineata* from Mexico, is unfounded. Four of 7 Mexican specimens of *S. t. temporalineata*, including the holotype, have such marks (57%). Similar markings occur in 31 of 54 specimens of *S. t. limnetes* (also 57%). As is indicated in Figure 2, the number of labials so marked varies from 0 to 5 but there is no indication that *S. t. limnetes* differs from the other populations of *Storeria tropica* in this respect.

Distribution.—*Storeria tropica limnetes* occurs in the salt marshes of the gulf coast of Louisiana and Texas. It is abundant in the Mississippi delta and its eastern limit is apparently Lake Ponchartrain, although it may extend to the mouth of the Pearl River. The western limit of range presently recorded is Galveston Co., Texas.

Habitat.—Within the marshes *S. t. limnetes* may be found under logs and debris on natural levees. Dr. Fred Cagle tells me he has often found individuals in muskrat houses in the open marsh.

Specimens examined.—TU 11374 (holotype). *Topotypic series* from the settlement of Waggaman, Harahan, St. Charles Parish, Louisiana: TU 11570, TU 14063, TU 11893, TU 11762, TU 11762a, TU 11762b, TU 11374a, TU 11374b. *Other specimens examined*: TU 14217, TU 11312, TU 11313, TU 14319, TU 12051, TU 3996, TU 6098, TU 6099, TU 3990-5, TU 3997-8, TU 4001, TU 4003-4, TU 3989, TU 11503, TU 11535, TU 11535a, TU 11535b, TU 11160, TU 7515, TU 14236, TU 7519, TU 6097, TU 10862, TU 11373, TU 6035. UMMZ 86510, MVZ 8162, MVZ 8157, BCB 3883, BCB 4234, REE A-97, REE A-162, USNM 55913, USNM 73828, USNM 15377, USNM 4798a, USNM 5199, USNM 13090.

DISCUSSION

Storeria tropica, if the conclusions of the present study are correct, is a distinct species closely related to *Storeria dekayi*. It is subtropical to tropical in range and in general appears to be a lowland form with mesic requirements. On the basis of the evidence at hand it appears to have diverged from *S. dekayi* or a common ancestor in the southern part of the present range, but a better understanding of the status and distribution of the southern populations of both species is needed before the time and place of differentiation of *Storeria tropica* can be evaluated. The question of the status of *Storeria dekayi victa*, which should be reconsidered in the light of the color pattern resemblance to *S. tropica*, may in turn bear on the history of the latter species.

The disjunction of *Storeria tropica limnetes* from the southern

populations seems, on morphological grounds, to have been of recent occurrence. Blair (1958) has interpreted present and past disjunct distributions along the Gulf Coastal plain as evidence of Pleistocene cooling. In view of the present distribution of *Storeria tropica*, the existence of populations along the now arid coastal hiatus would require more mesic environments and temperature change need not enter into the problem directly. Blair devotes relatively little attention to the pluvial periods and their significance, but infers from the occurrence of Pleistocene fossils of *Neofiber* in the Texas panhandle and in Kansas, and of *Capybaras* (*Hydrochoerus* and *Neochoerus*) in Florida, that mesic communities must have existed at some time during the Pleistocene in presently arid areas.

Martin and Harrel (1957), in their discussion of the cloud forest biota of northern Mexico, have concluded that the evidence does not support the occurrence of a cool moist forest corridor during the Pleistocene across the now arid parts of Texas. They suggest, however, that Pleistocene pluvial periods could have resulted in savannah formations and in colonization of expanded river flood plains by mesophytic vegetation. During such intervals of increased stream flow the establishment of marshes or of mesic communities permitting the spread of *Storeria tropica* along the Laguna Madre seems likely. The isolation of Louisiana and East Texas populations was probably initiated in the Hypsithermal, for which Martin (1958) cites the interval between 9,500 and 2,000 years ago.

The sympatry of *Storeria tropica limnetes* and *Storeria dekayi* along the ecotone between the marshes and the communities on higher ground is an inviting problem in the study of isolating mechanisms, particularly in comparison with the situation in the genus *Natrix* in the same area. It may be that both sympatry and hybridization are associated with ecologically disturbed environments. This is an evolutionary pattern which promises to increase in importance in the future.

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Notes and Discussion

"Single-Needled" Loblolly Pine

A loblolly pine (*Pinus taeda* L.) whose fascicles each contain a single, straight, terete needle has been growing for three years in a plantation in eastern Tennessee. Normal trees have 2, 3, or 4 separate and slightly twisted needles in each fascicle.

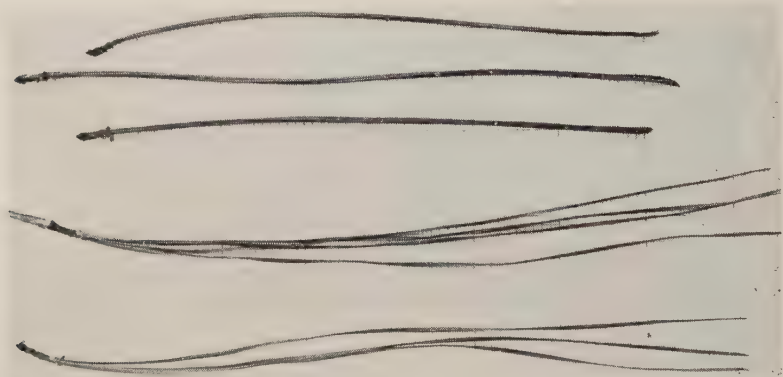


Fig. 1.—Cohering loblolly pine needles at top, normal at bottom.

Each "single needle" consists of 2 to 4 separate ones tightly cohering along their adaxial surface, somewhat similar to a sand pine, *Pinus clausa* (Chapm.) Vasey, reported from Florida (Woods and Dawsey, 1955. *Bot. Gaz.*, 116:292). The component leaves are not cellularly joined but seem held together by some natural adhesive. With care they can be stripped part. From a distance, the tree seems covered with long, green spikes.

Otherwise the tree is normal. The seed-source is unknown. It is one of several thousand loblolly seedlings obtained from the State Nursery at Pinson, Tennessee, and planted at Sewanee in February 1957. No other survivors of the shipment manifest the peculiarity.—T. A. HARRINGTON, Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, New Orleans 13, La.

Further Remarks on the Collembolan Genus *Hypogastrura* with Description of a New Genus

In a previous issue (Yosii, 1960) I discussed the subdivision of the collembolan genus *Hypogastrura* from the chaetotaxical point of view and described certain species. The manuscript was completed and in press, so that I could not refer to the important and interesting notes of Dr. P. Casagnau (1959). His conclusions parallel mine, but he has recognized *Ceratophysella* as a separate genus from *Hypogastrura*. I regard this change as reasonable and further believe that the subgenus *Cyclograna* (Yosii, 1960) should be elevated to generic rank:

Cyclograna gen. n.

Generic type.—*Hypogastrura vulgaris* Yosii, 1960.

Diagnosis.—Near to *Ceratophysella* Börner 1932. But the accessory tubercle of the postantennal organ is surrounded by two posterior tubercles.

At the same time Cassagnau has divided the genus *Ceratophysella* into two groups: A-type and B-type, which are identical with my *communis*-group and *armata*-group, respectively. His *C. denticulata* (Bagnall) seems to be near to my *C. exilis* (Yosii), although it is not yet certain whether his *C. denticulata* is Bagnall's species, a fact which is not exactly to be determined.

Recent material from the United States in a collection donated by Prof. F. Bonet of Mexico is under study at the moment. In this collection, there are some specimens which are identified as *Ceratophysella pseudarmata* (Folsom). The species which I described under *H. pseudarmata* previously (Yosii, 1960) represents a new species designated as follows:

***Ceratophysella brevisensillata* sp. n.**

Syn.: *Hypogastrura pseudarmata* (nec Folsom) Yosii, 1960.

Diagnosis.—As described in my previous paper (Yosii, 1960: 261, Figs. 4, 24-29).

Holotype.—A male from Arlington, Massachusetts, USA. (15 XI 1950, K. Christiansen).

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—RIOZO YOSII, Yoshida College, Kyoto University, Japan.

Book Reviews

A GATHERING OF SHORE BIRDS. By Henry Marion Hall. Edited and with additions by Roland C. Clement. The Devin-Adair Co., New York. 1960. xii + 242 pp., 95 figs., all pen-and-ink drawings. \$10.00.

This book is primarily a series of Hall's articles, many of which have appeared in *Audubon Magazine*. Clement has added to many species accounts and has supplied valuable sections on An Introduction to the Shore Birds, The Shore Bird Families, The South American Shore Birds, and The Wanderers. Clement states that the aim "is to bring Dr. Hall's essays up to date in a series of comments on recent changes of status which have occurred, and to interpolate some of the more readable scientific commentaries gleaned from a perusal of an extensive literature in order to introduce the non-professional reader to a particularly attractive group of birds." This objective has been attained.

Readable and interesting individual accounts of "57 Shore Birds Breeding in North America" north of the Panama Canal comprise 202 pages. Habits, habitats, plumages, field marks, behavior, local names, and ranges are discussed for each species. Hall has based many of his observations on experiences along the Atlantic coast, where he has hunted and observed shorebirds. Clement's contributions improve and round out this section. Emphasis is placed on the increase of shorebirds after they were protected from hunting. Lay readers will enjoy the section on South American shorebirds and the lists of North American species which share their ranges with South America, Europe, and Asia. Except for that of the dead Eskimo Curlew (p. 11), most of the line drawings by John Henry Dick are pleasing and add to the book.

Of the "breeding" species discussed in some detail, the Ruff and Curlew Sandpiper are not known to nest in North America. I found many of the local names of shorebirds unfamiliar and confusing when used interchangeably in the text. There are minor inconsistencies in the usage of "accepted" vernacular names — "Hudsonian Whimbrel," "Whimbrel," or "Hudsonian Curlew" for Whimbrel; "Wilson's Snipe," "Wilson's Common Snipe," and "Common Snipe" for the latter; "Tatler" and "Tattler," each repeated several times. Banding studies have not substantiated that Black Oystercatchers "mate for life" (p. 34). One doubts that American Woodcocks can be sexed upon flushing (p. 85) or that Black-bellied Plover tracks are larger than those of the Ruffed Grouse (p. 67).

Under "American Shore Birds in Europe," the American Avocet is included because it is accidental in Greenland, but under "European Shore Birds in America," the European Oystercatcher, Eurasian Golden Plover, and Redshank are listed only because they occur in Greenland.

All of these minor criticisms do not detract greatly from the value of the volume, and those for whom it is intended will find much informative and enjoyable reading in it.—RUSSELL E. MUMFORD, Purdue University, Lafayette.

ECOLOGY OF INLAND WATERS AND ESTUARIES. By George K. Reid. Reinhold Publishing Corp., New York. xi + 375 pp., 100 figs., 12 tables. 1961. \$7.50.

Flowing waters have been neglected in limnology texts. Dr. Reid's book attempts to present a balanced treatment of both lakes and streams as well

as estuaries. Part I considers physiography and sediments; Part II, water and its properties; Part III, light, heat, hydrography, dissolved gases, and solids; Part IV, aquatic organisms, discussed in phylogenetic sequence; and Part V, populations and aquatic communities. The selection of subject matter and the relative attention given the various disciplines is satisfactory. Biogeography, evolution, and problems of species abundance are mentioned only incidentally. The floristic and faunistic survey is restricted to the United States, with a few exceptions.

The book is written for undergraduate students with little scientific background, so that much of the text is devoted to explaining elementary facts and principles of geology, physics, chemistry, and biology. Furthermore, citations to the bibliography (which is adequate) are seldom given in the body of the text. These two features render the book unsuitable for advanced students or as a reference for applied limnologists.

Although Reid's prose will make the purist cringe, the sentences are short and crisp, and usually readily understandable. Poor definitions and errors of fact are too numerous; e.g., "discharge" and "potential natality" are incorrectly defined; the freshwater mysid, *Taphromysis*, is overlooked, and *Craspedacusta* is said to have been introduced from South America or the West Indies.

The physical makeup is attractive and the figures are good. The instructor who is courageous enough to teach limnology at the sophomore or junior level will find this text useful.—ALFRED E. SMALLEY, Tulane University, New Orleans, Louisiana.

LIVINGSTONE'S PRIVATE JOURNALS 1851-1853. Edited by I. Schapera. University of California Press, Berkeley and Los Angeles. XXIV — 341 pages, including 3 maps. 1960. \$5.00.

This is the first complete publication of Livingstone's records of two journeys to Northern Rhodesia only slightly more than a century ago. For anyone interested in historical data for purposes of evaluating the biological changes that have taken place in Africa in so short a segment of history, Livingstone's records are essential and usually engagingly written.

Although the name of Livingstone is associated with missionary activities in Africa, these journals amply testify that he was also an adventurous naturalist and explorer, so much so that the intrusion of gospel moralizing is excusable. Although Livingstone's own observations on plants and animals are excellent, his deductions are often influenced by the knowledge of his times thus providing the reader with an extra dividend of historical value. His account of the biology of the tsetse fly and its distribution is of great interest and so also are his observations on the "bullfrog"; tree rings of the baobab and its age; bushman arrow poison and the eastwardly distribution of these people; hornbill nesting habits, probably the first to be published; the wide-spread use of *Cannabis sativa*; termite flights; and the habits of the tick bird.

Of great interest are his medical comments; his credulity with respect to native folklore; his criticism of native superstitions that differ so little from some of his own; and his comment on the approaching "Golden Age" of civilization; and his use of "alligator" for crocodile, and "tiger" for leopard, usage that one still encounters among nontechnical people.—R. B. COWLES, University of California, Los Angeles.

PRINCIPLES OF ANIMAL TAXONOMY. By George Gaylord Simpson. Columbia University Press, New York, N. Y. 247 p., 1961. \$6.00.

Professor Simpson states categorically that the title of this book is to be taken literally. "The subject is principles, and particular groups of organisms or classifications thereof are involved only as examples and as the basis for inductive derivation of principles. The principles are those of taxonomy, as strictly defined hereinafter. . . . The kind of taxonomy involved is explicitly that applicable to animals, by which I mean metazoans. Most of the same principles apply to plants and many of them, with less generality, to protists. Although such applications may be mentioned in passing, they are largely incidental. Examples are drawn principally from mammals, for personal and practical reasons. Principles derived from and applicable to mammals are sufficiently general from all Metazoa that the word 'animal' in the title should not constitute false advertising, but a specialist in, say, coelenterates may quite properly reach some other conclusions in the light of his different experience."

The reviewer, a taxonomic botanist, having duly noted in the introductory paragraphs that most of the principles apply to plants, soon wished that the author had been less modest, had eliminated the word "animal" from the title, and had not cared a hoot about advertising one way or the other. Were the reader, if a botanist, to cross in his mind's eye the word "animal" from the title, to substitute in the text in appropriate places the word "plant" for "animal," the word "botanical" for "zoological," etc., he could scarcely wish for a better discussion of the principles pertinent to taxonomic botany. My comments, then, relate to the particular value the book seems to me to have for botanists.

As a teacher-student of plant taxonomy, I have often wished for a comprehensive, unified treatise on taxonomic principles. One can, of course, read (and have his more advanced students read) numerous shorter essays and various papers and books which one way or another elucidate certain of the taxonomic principles. This, however desirable in a complimentary fashion, is no satisfactory substitute for a searching, lucid, coherent exposition of the principles in an over-all context. There are botanical textbooks of relatively recent vintage having the word "taxonomy" in their titles. None of these books is primarily about taxonomy in the sense of Simpson (see p. 11). Certainly their authors purport to treat taxonomic principles, among other things, but one is hard put to it to divine what precisely it is they consider those principles to be.

Not the least service done by Simpson in his book is that of establishing precisely what is meant (at least by him) by systematics, taxonomy, classification, and nomenclature. It would seem that these terms, so commonly employed, so basic to communication in biology, would hardly require a full chapter for their proper definition. The hash that has, in general, been made with them is only exceeded by (thank goodness!) the clarity with which they are here ordered. This logical general terminology, if adopted and not quibbled over, has much virtue.

The history of classification and of taxonomy is more often than not presented as a dry, dull detailing of significant milestones or of the names of significant persons, their birth dates and death dates, and a few dusty dribbles as to their contributions. Simpson with refreshingly uncommon facility reviews the history of concepts, ideas, and systems pertinent to the historical origins of and development of current taxonomic thought.

The author's ambitious objectives include examination of the "deepest

foundations" of taxonomy and the hope that students may be provided with rudiments with which to learn to think about taxonomy and not just to do it. His well integrated discussions comprise an eminently successful achievement of these purposes. And the web is so nicely woven it seems hazardous to single out some threads for examination.

In view of the many prior disputations regarding the species concept, and despite recent relative agreement on a so-called "biological" or genetical concept, the section on the species and lower categories has much to offer in the way of a rational appraisal. For those of us (perhaps mostly botanists) who have objected to dependence on the single criterion of interbreeding (or lack of it) in formulation of a definition, the cockles of our hearts are tickled by: "Species do evolve, and almost always do so gradually. Among evolutionary species there cannot possibly be a general dichotomy between free interbreeding and no interbreeding. . . . To insist on an absolute objective criterion would be to deny the facts of life, especially the inescapable fact of evolution." Elsewhere (p. 110) Simpson says that a basic principle of taxonomy is that its results should be useful. If recognition of species as such has any value in biological communication, then of necessity a flexible concept must be derived from the somewhat less than static facts of life. In these regards there is an illuminating discussion apropos of species in uniparental organisms. One can but wish that apomixis of the variety of kinds known in plants occurred also in animals so that we might have the benefit of Simpson's critical analysis on this too.

This book will provide the teacher of a course in taxonomy, animal or plant, wherein it is neither desired nor intended that his students merely perform exercises in identification or limited classification, a stimulating, thought-provoking, and comprehensive discussion of the theoretical bases, principles, procedures, and rules of the subject. Suitable examples can readily be provided by the instructor from his own different experience with which to illustrate.

This book is sufficiently free of jargon so that the reader need not become afflicted with hardening of the categories.—R. K. GODFREY, Department of Biological Sciences, Florida State University.

Books Received

A SURVEY OF VARIOUS LATE CENOZOIC VERTEBRATE FAUNAS OF THE PANHANDLE OF TEXAS. Part III. Felidae. By Donald E. Savage. University of California Press. 28 p., 7 text figs. 1960.

STRATIGRAPHY AND PALEONTOLOGY OF THE PERMIAN NOSONI AND DEKKAS FORMATIONS (BOLLIBOKKA GROUP). By Alan H. Coogan. University of California Press. (Univ. Calif. Publ. Geol. Sci., 36(5):243-316, 5 pls., 23 text figs.). 1960. \$1.75.

A MARINE CARNIVORE FROM THE CLALLAM MIOCENE FORMATION WASHINGTON. By R. A. Stirton. University of California Press. (Univ. Calif. Publ. Geol. Sci., 36(7):345-368, 4 text figs.). 1960. \$0.75.

GUIDE TO THE STUDY OF THE ANATOMY OF THE SHARK, NECTURUS, AND THE CAT. 3rd ed. By Samuel Eddy, Clarence P. Oliver and John P. Turner. John Wiley & Sons, Inc., New York. viii + 141 p. 1960. \$3.50.

THE MECHANISM OF EVOLUTION. By W. H. Dowdeswell. Harper Torchbooks: The Science Library. Harper and Brothers, New York. 115 p. 1960. \$0.95.

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- MULTIVARIATE ANALYSIS OF PLEISTOCENE AND RECENT COYOTES (*CANIS LATRANS*) FROM CALIFORNIA. By Eugene Giles. University of California Press. (Univ. Calif. Publ. Geol. Sci., 36(8):369-390, 4 text figs.). 1960. \$0.75.
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- THE MONARCH BUTTERFLY. By F. A. Urquhart. University of Toronto Press, Toronto. 361 p. 79 figs., 12 plates. 1960. \$6.50 cloth; \$3.95 paper.
- HERBICIDES AND THE SOIL. Edited by E. K. Woodford and G. R. Sagar. Blackwell Scientific Publications, Oxford. 88 p. 1961. \$3.50.
- THE AMATEUR SCIENTIST. By C. L. Strong. Introduction by Vannevar Bush. Simon and Schuster, New York. 584 p., 256 text figs. 1960. \$5.95.
- SCIENTIFIC WORDS: THEIR STRUCTURE AND MEANING. By Dr. W. E. Flood. Duell, Sloan and Pearce, New York. 220 p. 1960. \$3.50.
- THE RELATIONSHIP OF THE PEARY AND BARREN GROUND CARIBOU. By T. H. Manning. Arctic Institute of North America, Technical Paper No. 4. 52 p., 9 figs. 1960. \$2.00.
- MARINE INFAUNAL BENTHOS IN ARCTIC NORTH AMERICA. By Derek V. Ellis. Arctic Institute of North America, Technical Paper No. 5. 53 p. 17 figs. 1960. \$2.00.

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 66

OCTOBER, 1961

No. 2

An Annotated List of Fishes from the Coosa River System of Alabama¹

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ABSTRACT: A survey of the fish fauna of the Coosa River drainage, a major tributary of the Alabama system, was conducted in June, 1959. Collections were made at 44 stations. The results of these and 10 collections made in previous years, plus records from the literature, show the fish fauna of the Coosa drainage of Georgia and Alabama to comprise 20 families and 85 species. Ten species are endemic to the upper Alabama system, and 10 represent new records for the Coosa drainage. Each collecting station is described and the species collected are listed. Annotations include notes on the morphology, color, and ecology of many of the species. The number of specimens collected at each station, and the size ranges are given for each species. A bibliography for each species is also included.

The Coosa River is formed by the confluence of the Etowah and Oostanaula rivers at Rome, Georgia. It flows in a southwesterly direction almost to Montgomery, Alabama where it joins with the Tallapoosa to form the Alabama. The Alabama River meets the Tombigbee to form the Mobile, the largest Gulf drainage east of the Mississippi.

The purpose of this paper is to present data on the presence and distribution of the fishes of the Coosa River system which, along with similar data from other southeastern streams, will eventually result in establishing zoogeographic patterns, and which will contribute to our understanding of the divergence of the upper Mobile basin fish fauna from that of the Tennessee from which it presumably originated.

The first paper on the fishes of the Coosa River system was published by David Starr Jordan in 1877. Jordan listed 56 species from tributaries of the Etowah and Oostanaula Rivers in the vicinity of Rome, Georgia. Forty-six of Jordan's fishes are recognized as valid species. Twelve of the 13 species he described as new are recognized as valid species today. Jordan and Brayton (1878) expanded this list to include the entire Alabama basin and added one species to the list of known fishes of the Coosa River. In another paper, Jordan (1879) listed fishes from the Etowah River. Gilbert's (1891) report was the first to include fishes from the Coosa River of Alabama. Fowler's (1945) records are from Dekalb and Cherokee Counties, Alabama,

¹ This project was supported by a grant from the University of Alabama Research Committee.

and Scott's (1951) are from the Coosa River near Childersburg, Alabama. These and all other literature records of fishes of the Coosa River system known to the author are included in the synonymies. Based on these data and those obtained as a result of this research, 84 species are definitely known to occur in the Coosa River system, plus those listed herein as probable or doubtful.

Acknowledgments.—I wish to acknowledge the assistance of Robert E. Smith in collecting the material for this paper, and the encouragement and advice from Ralph L. Chermock during the writing of the report. Appreciation is also due Royal D. Suttus for identifying specimens of *Notropis bellus* and *N. lirus*, along with several darters, including an apparently unnamed species in the subgenus *Ulcocentra*.

MATERIALS AND METHODS

In June, 1959, Robert E. Smith and I collected in the Coosa drainage of Alabama as part of a continuing survey of the fish fauna of the Mobile basin conducted by the University of Alabama. Ten collections from the Coosa were made in previous years; to these, we add 44 more stations. These are numbered in sequence from north to south (Figure 1). Each station was thoroughly sampled until the collectors were convinced that subsequent trials would probably not yield additional species. Dissolved oxygen was determined by the Alsterberg (Azide) modification of the Winkler method as described by Lagler (1956). Counts and measurements were made according to the method of Hubbs and Lagler (1947).

The following abbreviations are used in addition to the standard compass directions: T = townships, R = range, sec. = section, elev. = elevation, C = centigrade, ppm = parts per million, mm = millimeters, Co. = County, R = River, Cr. = Creek, trib. = tributary, UAIC = University of Alabama Ichthyological Collection (the Accession Number follows).

The number of specimens and the range of total length in millimeters are indicated in parentheses following the station number in the annotated list. For example, (12, 52-68) means 12 specimens ranging from 52 to 68 millimeters in total length. Ranges, townships, sections, and elevations were determined from U. S. Geological Survey Maps (AMS series), scale 1: 250,000. Elevations are given in contour intervals of 100 feet above 1000 foot elevations and in intervals of 50 feet below 1000 foot elevations.

COLLECTION STATIONS IN THE COOSA RIVER DRAINAGE OF ALABAMA

Station 1. West Fork Little River, T 6 S, R 10 E, sec. 19; elev. 1500 feet; Desoto State Park, 7 miles south of Mentone, Dekalb Co., June 4, 1959. Water clear; current moderate to fast; bottom bed rock; depth 3 feet; width 30 feet. Water temperature 19.5°C; dissolved

oxygen 8.8 ppm. Method of capture: cast net. UAIC 632. Species²: 31.

Station 2. A branch tributary to West Fork Little River, T 6 S, R 10 E, sec. 30; elev. 1500 feet; 8 miles south of Mentone, Dekalb Co., June 4, 1959. Water clear; current still to moderate; bottom mud; depth 1 foot; width 12 feet. Water temperature 17°C; dissolved oxygen 8.5 ppm. Method of capture: seine. UAIC 633. Species: 24 and 67.

Station 3. Little River, T 7 S, R 10 E, sec. 30; elev. 1200 feet; 2.5 miles north of Blanche, on Cherokee-Dekalb Co. line, June 4, 1959. Water clear; current moderate to swift, with still pools above water fall; bottom bed rock. Collections were made with cast net in pools near shore. UAIC 674. Species: 62.

Station 4. Sells' Cave, T 9 S, R 7 E, sec. 4; elev. 700 feet; 3 miles west of Collinsville, Dekalb Co., June 29, 1958. Water crystal clear. Water temperature 14°C. Water depth at entrance of cave approximately 10 feet. Water is not known to flow from the cave. Big Wills Creek is about 400 feet south of the cave at an elevation of 650 feet. Collectors: Robert E. Smith, Jesse White and Herbert Boschung. Method of capture: dip net. UAIC 656. Species: 53.

Station 5. Little Creek, tributary of Big Wills Creek, T 9 S, R 7 E, sec. 8; elev. 700 feet; 3.5 miles west of Collinsville, Dekalb Co., June 3, 1959. Water turbid following rain; current moderate to fast; bottom mostly gravel, some soft clay; depth 1.5 feet; width 10 feet. Water temperature 20°C; dissolved oxygen 8.5 ppm. Method of capture: seine. UAIC 631. Species: 22, 24, 36, 62, and 81.

Station 6. Big Wills Creek, 10 miles northeast of Attalla, Etowah Co., June 5, 1953. Water turbid; current swift; bottom sand, rock and mud; width to 30 feet. Water temperature 18°C. Collector: L. B. Cooper. Method of capture: seine. UAIC 477. Species: 27, 74, 78, and 85.

Station 7. Clear Creek, tributary of Big Wills Creek, 5 miles northeast of Gallant, Etowah Co., July 27, 1955. Water clear; width 15 feet. Collector: Henry Howell. Method of capture: seine. UAIC 457. Species: 22, 24, 35, 36, 37, 45, 54, 78, 81, and 85.

Station 8. Big Wills Creek, 5 miles west of Gadsden, Etowah Co., June 5, 1953. Water turbid; current swift; bottom rock, sand and mud; depth to 4 feet; width to 40 feet. Water temperature 22°C. Collector: L. B. Cooper. Method of capture: seine. UAIC 476. Species: 16, 67, and 68.

Station 9. Nances Creek, T 14 S, R 9 E, sec. 2; elev. 900 feet; 6.5 miles north of White Plains, Calhoun Co., June 5, 1959. Water slightly turbid; current moderate to swift; bottom silt and rock; depth 1 foot; width 12 feet. Water temperature 19°C; dissolved oxygen 8.5 ppm. Method of capture: seine; cast net. UAIC 634. Species: 22, 24, 31, 35, 45, 62, 64, 75, 78, and 81.

² The numbers refer to the annotated list of species to follow.

Station 10. Nances Creek, T 12 S, R 10 E, sec. 33; elev. 600 feet; one mile northeast of Piedmont, Calhoun Co., July 23, 1949. Collector: Ben Sanders. Method of capture: seine. UAIC 36. Species: 22.

Station 11. Terrapin Creek, T 12 S, R 10 E, sec. 27; elev. 650 feet; 3 miles northeast of Piedmont, Cherokee-Calhoun Co. line, July 9, 1949. Collector: Ben Sanders. Method of capture: seine. UAIC 37. Species: 22 and 30.

Station 12. Terrapin Creek, T 11 S, R 10 E, sec. 20; elev. 600 feet; Coloma, Cherokee Co., June 4, 1959. Water moderately muddy; current slow; bottom clay and gravel; depth 1 foot; width 10 feet. Method of capture: seine. UAIC 675. Species: 56.

Station 13. Little Canoe Creek, T 12 S, R 4 E, sec. 21; elev. 800 feet; 2 miles south of Gallant. Etowah-St. Clair Co. line, July 29, 1955. Collector: Henry Howell. Method of capture: seine. UAIC 459. Species: 35, 67, 68, and 81.

Station 14. Little Canoe Creek, T 12 S, R 4 E, sec. 25; elev. 800 feet; 2.5 miles northeast of Steele, Etowah-St. Clair Co. line, July 28, 1955. Collector: Henry Howell. Method of capture: seine. UAIC 458. Species: 17, 27, 28, 35, 37, 39, 45, 61, 67, 68 and 81.

Station 15. Big Canoe Creek T 14 S, R 2 E, sec. 13; elev. 900 feet; one mile east of Caldwell, St. Clair Co., June 15, 1959. Water turbid; depth 8 feet, width 30 feet. Method of capture: cast net. UAIC 649. Species: 16, 29, 55, 66, and 68.

Station 16. South Fork of Big Canoe Creek, T 15 S, R 1 E, sec. 1; elev. 900 feet; 2 miles west of Springville, St. Clair Co., June 15, 1959. Water clear; current slow to moderate; bottom small rock and gravel; depth 1.5 feet; width 8 feet. Water temperature 19.5°C; dissolved oxygen 8.4 ppm. Method of capture: seine; cast net. UAIC 648. Species: 16, 22, 31, 33, 36, 37, 41, 45, 54, 55, 68, and 81.

Station 17. Big Canoe Creek, T 14 S, R 4 E, sec. 6; elev. 900 feet; one mile east of Ashville, St. Clair Co., June 15, 1959. Water turbid; current slow to moderate; bottom mud; depth 3 feet; width 20 feet. Method of capture: cast net. UAIC 650. Species: 29, 30, and 68.

Station 18. Perimeter Creek, T 13 S, R 5 E, sec. 34; elev. 600 feet; 2 miles northwest of Greensport, St. Clair Co., June 16, 1959. Water slightly muddy; current slow; bottom mud; depth 3 feet; width 20 feet. Water temperature 21°C; dissolved oxygen 7.5. Method of capture: cast net. UAIC 652. Species: 37, 41, 55, 56, 66, 67, 68, and 71.

Station 19. Near mouth of Beaver Creek, T 14 S, R 5 E, sec. 1; elev. 600 feet; Greensport, St. Clair Co., June 16, 1959. Water turbid, current slow; bottom mud; depth 5 feet; width 20 feet. Water temperature 20.5°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 651. Species: 28, 31, 33, 37, 39, 41, 45, 56, 67, and 68.

Station 20. Near mouth of Shoal Creek, T 14 S, R 5 E, sec. 13;

elev. 600 feet; 2 miles south of Greensport, St. Clair Co., June 16, 1959. Water slightly muddy; current moderate; bottom rocky; depth 1.5 feet; width 20 feet. Water temperature 21°C; dissolved oxygen 7.8 ppm. Method of capture: seine; cast net. UAIC 653. Species: 16, 22, 28, 29, 30, 31, 33, 41, 45, and 68.

Station 21. Near mouth of Bridge Creek, T 14 S, R 6 E, sec. 30; elev. 500 feet; 4 miles south of Greensport, St. Clair Co., June 16, 1959. Water muddy; current very slow; bottom mud; depth 5 feet; width 20 feet. Method of capture: cast net. UAIC 654. Species: 74.

Station 22. Broken Arrow Creek, T 16 S, R 4 E, sec. 5; elev. 500 feet; 7.5 miles southwest of Ragland, St. Clair Co., June 16, 1959. Water slightly turbid; current slow to moderate; bottom rock and mud; depth 3 feet; width 20 feet. Water temperature 19.5°C; dissolved oxygen 7.4 ppm. Method of capture: seine; cast net. UAIC 655. Species: 10, 17, 29, 33, 36, 39, 45, 55, 61, 67, 68, 75, and 85.

Station 23. Choccolocco Creek, T 15 S, R 9 E, sec. 22; elev. 700 feet; 1 mile east of Pleasant Ridge, Calhoun Co., June 5, 1959. Water moderately turbid; current still to moderate; bottom silt and mud; depth to 8 feet; width to 60 feet. Water temperature 19.5°C; dissolved oxygen 8.3 ppm. Method of capture: seine; cast net. UAIC 635. Species: 10, 16, 22, 24, 28, 29, 32, 35, 37, 54, 56, 63, 64, 70, and 85.

Station 24. Choccolocco Creek, T 15 S, R 9 E, sec. 27; elev. 700 feet; 1.5 miles north of Iron City, Calhoun Co., June 5, 1959. Water clear; current moderate to swift; bottom gravel and sand; depth 1 foot; width 8 feet. Water temperature 19.5°C; dissolved oxygen 8.5 ppm. Method of capture: seine; cast net. UAIC 636. Species: 22, 31, 35, 36, 45, 54, 62, and 81.

Station 25. Cane Creek, T 15 S, R 8 E, sec. 17; elev. 600 feet; Fort McClellan, Calhoun Co., August 5, 1949. Method of capture: seine. UAIC 46. Species: 45.

Station 26. Cane Creek, T 15 S, R 7 E, sec. 11; elev. 700 feet; 6 miles north of Anniston, Calhoun Co., June 9, 1959. Water moderately turbid; current slow to moderate; bottom mud and gravel; depth 1.5 feet; width 15 feet. Water temperature 21.5°C; dissolved oxygen 7.2 ppm. Method of capture: seine; cast net. UAIC 643. Species: 19, 35, 37, 41, 45, 56, 75, and 85.

Station 27. Chehaw-haw Creek above lake at Cheaha State Park, T 18 S, R 8 E, sec. 8; elev. 1200 feet; Cleburne Co., June 6, 1959. Water clear; current moderate to swift; bottom gravel and rock; depth 1 foot; width 7 feet. Water temperature 19°C; dissolved oxygen 9.0 ppm. Method of capture: seine; cast net. UAIC 638. Species: 24, 31, and 65.

Station 28. Chehaw-haw Creek below lake at Cheaha State Park, T 18 S, R 8 E, sec. 8; elev. 1200 feet; Cleburne Co., June 6, 1959. Water clear; current swift; moderately still pools; bottom gravel and rock; depth 1 foot; width 7 feet. Water temperature

22°C; dissolved oxygen 8.6 ppm. Method of capture: seine; cast net. UAIC 637. Species: 24, 63, 65, and 68.

Station 29. Chehaw-haw Creek, tributary of Lake Chinnabee, T 18 S, R 7 E, sec. 14; elev. 1000 feet; Talladega National Forest, Clay Co., June 8, 1959. Water clear; current moderate; bottom rocky; depth 2 feet; width 15 feet. Water temperature 22°C; dissolved oxygen 7.3 ppm. Method of capture: seine; cast net. UAIC 640. Species: 29, 30, 31, 33, 56, 65, 66, 68, and 85.

Station 30. Cheaha Creek, tributary of Chehaw-haw Creek, T 18 S, R 7 E, sec. 5; elev. 700 feet; 2 miles east of McElderry, Talladega Co., June 8, 1959. Water clear; current moderately swift, with still pools; bottom rock, gravel, sand and mud; depth 1 foot; width 15 feet. Water temperature 24.5°C; dissolved oxygen 7.2 ppm. Method of capture: seine; cast net. UAIC 639. Species: 16, 22, 24, 29, 30, 31, 35, 41, 54, and 68.

Station 31. Chehaw-haw Creek, tributary of Choccolocco Creek, T 18 S, R 6 E, sec. 1; elev. 600 feet; McElderry, Talladega Co., June 9, 1959. Water clear; current slow to moderate; bottom mud, silt and rock; depth 3 feet; width 18 feet. Water temperature 22°C; dissolved oxygen 7.4 ppm. Method of capture: seine; cast net. UAIC 641. Species: 22, 25, 27, 29, 31, 33, 36, 37, 39, 41, 45, 54, 55, 63, 67, 68, and 78.

Station 32. Salt Creek, tributary of Choccolocco Creek, T 17 S, R 7 E, sec. 20; elev. 500 feet; 1.8 miles east of Munford, Talladega Co., June 9, 1959. Water clear to slightly turbid; current slow to moderate; bottom mud, silt, gravel and rock; depth 2 feet; width 20 feet. Water temperature 21°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 642. Species: 16, 22, 24, 29, 37, 39, 45, 63, and 67.

Station 33. Talladega Creek, T 19 S, R 5 E, sec. 5; elev. 500 feet; 3 miles south of Talladega, Talladega Co., June 10, 1959. Water turbid; current moderate; bottom rock, gravel, and coarse sand; depth 2 feet; width 30 feet. Water temperature 22°C; dissolved oxygen 7.9 ppm. Method of capture: cast net. UAIC 644. Species: 16, 18, 22, 27, 29, 37, 39, 45, 67, 68, and 74.

Station 34. Weewoka Creek, T 20 S, R 4 E, sec. 2; elev. 500 feet; Winterboro, Talladega Co., June 10, 1959. Water clear; current slow to moderate; bottom rock and gravel; depth 1 foot; width 15 feet. Water temperature 19.5°C; dissolved oxygen 7.9 ppm. Method of capture: seine; cast net. UAIC 645. Species: 22, 25, 31, 35, 36, 37, 39, 41, 45, and 78.

Station 35. Clear Creek, T 19 S, R 2 E, sec. 15; elev. 500 feet; Vincent, Shelby Co., June 17, 1959. Water clear; current slow to moderate; bottom rock and gravel; depth 1.5 feet; width 20 feet. Water temperature 20°C; dissolved oxygen 7.8 ppm. Method of capture: seine; cast net. UAIC 657. Species: 16, 22, 24, 29, 31, 35, 36, 41, 45, 54, 65, 78, 81, and 85.

Station 36. Coosa River, T 20 S, R 3 E, sec. 18; elev. 450 feet;

one mile northwest of Childersburg on Talladega-Shelby County line, September 13, 1954. Water turbid; shore rock, sand and clay. Collector: Henry Howell. Method of capture: rotenone. UAIC 447. Species: 8, 14, 18, 25, 38, 46, 50, 60, 63, 82, and 84.

Station 37. A nameless creek, one mile from the Coosa River, T 20 S, R 2 E, sec. 15; elev. 450 feet; approximately 2.5 miles east of U. S. Hwy. 280, Shelby Co., June 10, 1959. Water slightly turbid; current slow to moderate; bottom mud; depth 1.5 feet; width 12 feet. Water temperature 24°C; dissolved oxygen 7.6 ppm. Method of capture: cast net. UAIC 646. Species: 23, 24, 29, 38, 45, 56, 62, 63, 67, 68, and 78.

Station 38. Four-mile Creek, T 20 S, R 1 E, sec. 25; elev. 500 feet; 1.5 miles north of Wilsonville, Shelby Co., June 17, 1959. Water clear; current slow to moderate; bottom rock and gravel; depth 1 foot; width 15 feet. Water temperature 22.5°C; dissolved oxygen 7.7 ppm. Method of capture: seine; cast net. UAIC 658. Species: 10, 22, 29, 31, 33, 36, 37, 41, 45, 56, 74, 75, 78, 81, and 88.

Station 39. Beeswax Creek, T 21 S, R 1 E, sec. 8; elev. 500 feet; 4.5 miles northeast of Columbiana, Shelby Co., June 17, 1959. Water slightly turbid; current slow; bottom rock and mud; depth 2 feet; width 10 feet. Water temperature 21°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 659. Species: 11, 17, 19, 33, 37, 41, 62, 64, 67, 68, and 74.

Station 40. Camp Branch of Waxahatchee Creek, T 22 S, R 1 W, sec. 6; elev. 500 feet; 5.5 miles southwest of Columbiana, Shelby Co., June 10, 1959. Water clear; current moderate; bottom rock and gravel; depth 1 foot; width 18 feet. Method of capture: cast net. UAIC 647. Species: 11, 33, 41, 55, 67, 74, and 83.

Station 41. Waxahatchee Creek, T 24 N, R 15 E, sec. 28, elev. 400 feet; 5 miles south of Shelby on Shelby-Chilton Co. line, June 17, 1959. Water clear; current moderate; bottom rock and gravel; depth 1 foot; width 15 feet. Water temperature 19°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 661. Species: 22, 35, 36, 45, 68, and 85.

Station 42. Waxahatchee Creek, T 24 N, R 15 E, sec. 25; elev. 400 feet; backwater of Lay Lake, Shelby Co., June 17, 1959. Water slightly muddy; currently still; bottom clay and gravel. Water temperature 25°C. Method of capture: cast net. UAIC 660. Species: 9, 55, 63, 66, 68, and 74.

Station 43. Channel of Coosa River, T 23 N, R 15 E, sec. 13; elev. 300 feet; 1 mile north of Lay Dam, Chilton Co., June 18, 1959. Water turbid; current still. Method of capture: basket traps in approximately 20 feet of water. UAIC 662. Species: 46 and 47.

Station 44. Yellowleaf Creek, T 23 N, R 15 E, sec. 17; elev. 400 feet; Jumbo, Chilton Co., June 18, 1959. Water clear; current moderate; bottom rock and gravel; depth 1 foot; width 20 feet. Water temperature 22.5°C; dissolved oxygen 8.3 ppm. Method of capture:

seine; cast net. UAIC 663. Species: 17, 29, 33, 35, 36, 37, 39, 40, 55, 63, 67, 74, and 81.

Station 45. Hatchet Creek, T 23 N, R 19 E, sec. 30; elev. 450 feet; 4 miles north of Rockford, Coosa Co., June 19, 1959. Water slightly turbid; current still to moderate; bottom silt and rock; depth 1.5 feet; width to 50 feet. Water temperature 23°C; dissolved oxygen 8.0 ppm. Method of capture: seine; cast net. UAIC 673. Species: 61 and 67.

Station 46. Swamp Creek, T 21 N, R 18 E, sec. 1; elev. 500 feet; 1.5 miles north of Pantenville, Coosa Co., June 19, 1959. Water slightly turbid; current slow to moderate; both sand and fine gravel; depth 1 foot; width 20 feet. Water temperature 21°C; dissolved oxygen 8.4 ppm. Method of capture: seine; cast net. UAIC 672. Species: 16, 29, 30, 34, and 39.

Station 47. Weoka Creek, T 20 N, R 18 E, sec. 2; elev. 500 feet; 4.5 miles south of Pantenville, on Coosa-Elmore Co. line, June 19, 1959. Water slightly turbid; current still to moderate; bottom silt. Water temperature 22°C. Method of capture: seine and cast net from shore. UAIC 671. Species: 22, 29, 30, 34, 37, 39, and 74.

Station 48. Little Weoka Creek, T 20 N, R 18 E, sec. 11; elev. 500 feet; 6.5 miles north of Riddle, Elmore Co., June 19, 1959. Water slightly turbid; current slow to moderate; bottom rock and gravel; depth 2 feet; width 10 feet. Water temperature 20.5°C; dissolved oxygen 7.5 ppm. Method of capture: cast net. UAIC 670. Species: 25, 29, 34, 37, and 76.

Station 49. Chestnut Creek, T 21 N, R 15 E, sec. 36; elev. 400 feet; Verbena, Chilton Co., June 18, 1959. Water slightly turbid; current moderate; bottom rock, gravel, and clay; depth 1.5 feet; width 30 feet. Water temperature 21°C; dissolved oxygen 8.4 ppm. Method of capture: seine; cast net. UAIC 664. Species: 17, 39, 68, and 74.

Station 50. West Branch of Shoal Creek, T 20 N, R 16 E, sec. 26; elev. 400 feet; 1 mile north of Wadsworth, Autauga Co., June 18, 1959. Water clear; current still to moderate; bottom rock and gravel; depth 1 foot; width 5 feet. Water temperature 21°C; dissolved oxygen 7.7 ppm. Method of capture: cast net. UAIC 665. Species: 22, 34, and 37.

Station 51. Coosa River below Jordan Dam, T 19 N, R 18 E, sec. 22; elev. 200 feet; Elmore Co., June 19, 1959. Water slightly turbid; current moderate to swift. Water temperature 21.5°C; dissolved oxygen 6.6 ppm. Method of capture: cast net from shore and by hook and line. UAIC 667. Species: 4, 6, 7, 8, 38, 46, 52, 55, 58, 59, 61, 66, and 68.

Station 52. Pigeonroost Creek, T 19 N, R 18 E, sec. 34; elev. 200 feet; 3.5 miles northwest of Wetumpka, Elmore Co., June 18, 1959. Water slightly turbid; current slow to moderate; bottom gravel; depth 1.5 feet; width 10 feet. Water temperature 23°C; dissolved

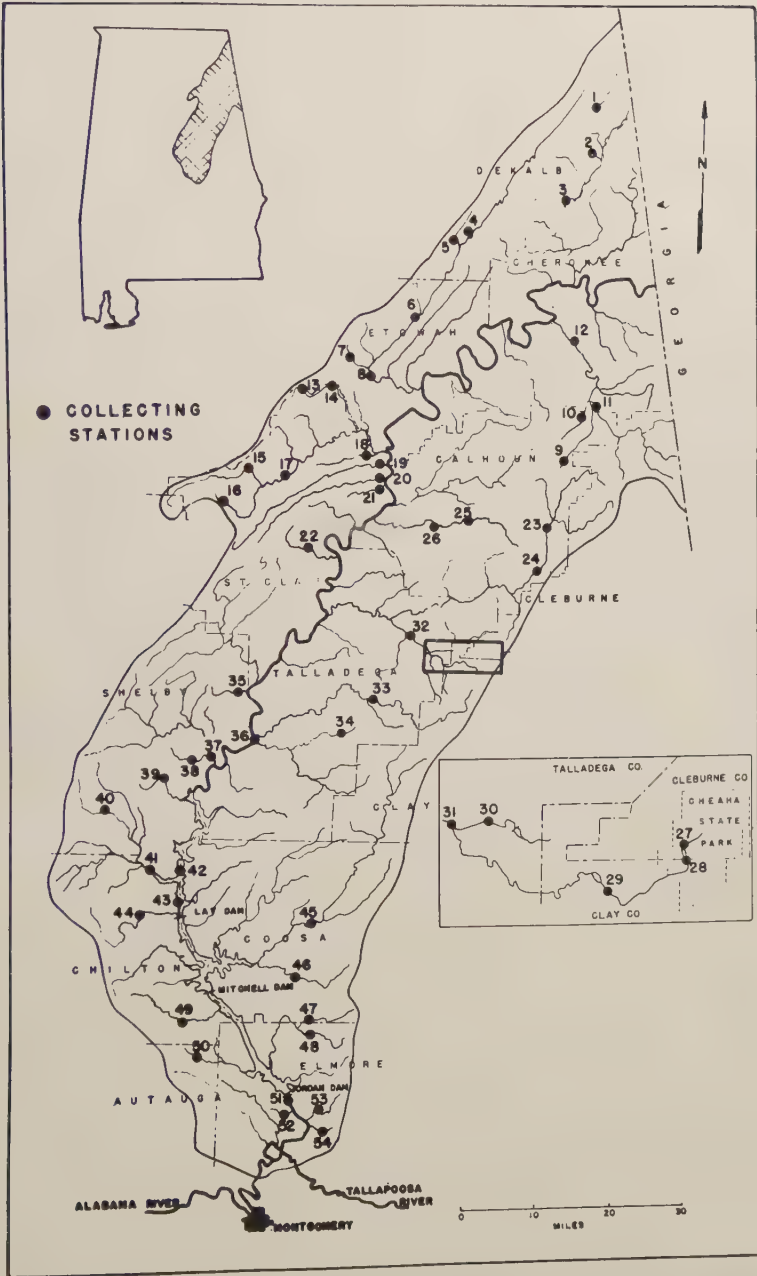


Fig. 1.—The Coosa River drainage of Alabama. The numbered collecting stations are described in the text.

oxygen 5.5 ppm. Method of capture: seine; cast net. UAIC 666. Species: 34, 40, 55, 63, 67, and 74.

Station 53. A nameless creek, T 18 N, R 19 E, sec. 6; elev. 200 feet; on east side of Coosa River, 3 miles north of Wetumpka, Elmore Co., June 19, 1959. Water slightly turbid; current moderate; bottom rock; depth 2 feet; width 25 feet. Water temperature 21.5°C; dissolved oxygen 8.3 ppm. Method of capture: seine; cast net. UAIC 668. Species: 18, 22, 23, 29, 37, 42, 45, 55, 62, 63, 67, and 68.

Station 54. A nameless creek, T 19 N, R 18 E, sec. 25; elev. 200 feet; on east side of Coosa River, 2.5 miles north of Wetumpka, Elmore Co., June 19, 1959. Water clear to slightly turbid; current slow; bottom sand and gravel; depth 1 foot; width 10 feet. Water temperature 21.5°C; dissolved oxygen 7.4 ppm. Method of capture: seine; cast net. UAIC 669. Species: 42 and 65.

ANNOTATED LIST OF SPECIES

PETROMYZONTIDAE—Lampreys

1. *Ichthyomyzon castaneus* Girard

Ichthyomyzon concolor.—Gudger, 1930: 145 (Coosa River, Rome, Ga.).

According to Hubbs and Trautman (1937), Gudger's specimens belong to this species. No new records.

2. *Ichthyomyzon gagei* Hubbs and Trautman.

Two records of this nonparasitic species are known from the Alabama River System. A paratype is from a tributary of the Alabama River in Wilcox Co. (Hubbs and Trautman, 1937), and Dendy and Scott (1953) collected them from several tributaries of the Tallapoosa River in Lee Co., Alabama. Although this lamprey has not been reported from the Coosa drainage, little doubt remains that it occurs there.

3. *Lampetra aepyptera* (Abbott)

Lampetra aepyptera.—Raney, 1952: 99 (tributary of Oostanaula River, Rome, Ga.).

No new records. This lamprey has not been collected from the Coosa drainage of Alabama, but it undoubtedly occurs throughout the Mobile basin. It has been reported by Cook (1952) from the Tombigbee and Pascagoula drainages, and by Cooper and Hemphill (1957) and Smith (1960) from tributaries of the Warrior River.

POLYODONTIDAE—Paddlefishes

4. *Polyodon spathula* (Walbaum)

The paddlefish was not seen by the author; however, a fisherman reported catching 22 "spoonbill cats" below Jordan Dam (station 51) on the night of June 18, 1959.

ACIPENSERIDAE—Sturgeons

5. *Acipenser fulvescens* Rafinesque

Acipenser fulvescens.—Scott, 1951: 31.

No new records.

LEPIDOSTEIDAE—Gars

6. *Lepisosteus osseus* (Linnaeus)

Lepisosteus osseus.—Jordan, 1877a: 369; Jordan and Brayton, 1878: 55; Jordan, 1879: 119.

Lepisosteus osseus.—Scott, 1951: 31.

One specimen measuring approximately 4 feet in total length was captured by hook and line at station 51.

CLUPEIDAE—Herrings

7. *Alosa chrysochloris* (Rafinesque)

Four specimens varying from 230 to 242 mm in total length were collected with the cast net at station 51.

8. *Dorosoma cepedianum* (LeSueur)

Dorosoma cepedianum heterurum.—Jordan, 1877a: 368.

Dorosoma cepedianum var. *heterurum*.—Jordan and Brayton, 1878: 49 (Montgomery, Ala.).

Dorosoma cepedianum.—Scott, 1951: 37.

Twelve specimens measuring from 95 to 123 mm were obtained with rotenone at station 36, and one 212 mm specimen was collected with a cast net at station 51.

9. *Dorosoma petenense* (Günther)

Four specimens measuring 50 to 56 mm were collected in the backwater of Lay Lake (station 42).

ESOCIDAE—Pikes

10. *Esox americanus* Gmelin

Esox raveneli.—Jordan, 1877a: 368.

Branchiostegal counts on 4 specimens were 13-14, 14-14, 14-14, and 14-15. *Esox americanus* and *niger* were not taken together but both seem to prefer still or slow currents.

Stations: 22 (2, 65-80); 23 (1, 171); 38 (1, 91).

11. *Esox niger* LeSueur

Esox reticulatus.—Jordan, 1877a: 324; Jordan and Brayton, 1878: 48; Jordan, 1879: 104.

Esox niger.—Fowler, 1945: 351.

Stations: 39 (1, 320); 40 (1, 250).

HIODONTIDAE—Mooneyes

12. *Hiodon tergisus* LeSueur

Hiodon selenops.—Jordan and Brayton, 1878: 48 (Alabama River, Montgomery, Ala.).

Hiodon tergisus.—Scott, 1951: 37.

No new records.

CATOSTOMIDAE—Suckers

13. *Cycleptus elongatus* (LeSueur)

Cycleptus elongatus.—Scott, 1951: 38.

No new records.

14. *Ictiobus bubalus* (Rafinesque)

? *Bubalichthys (taurus)*.—Jordan and Brayton, 1878: 55 ("Recorded by Professor Agassiz from the Alabama.").

Ictiobus bubalus.—Scott, 1951: 38.

Two specimens measuring 170 and 176 mm were collected at station 36.

15. *Carpiodes cyprinus* (LeSueur)

Carpiodes cyprinus.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 55 (Montgomery, Ala.).

No recent records.

16. *Moxostoma duquesnei* (LeSueur)

? *Moxostoma duquesnii* var. *duquesnii* (in part).—Jordan, 1877a: 349.

Moxostoma duquesnii.—Hubbs, 1930: 19 (Alabama River drainage of Georgia; description).

Jordan (1878) abandoned *duquesnei* as a distinct species and regarded the character of 10 pelvic rays as an individual character and not a specific one. Jordan's opinion was followed until Hubbs (1930) studied the group and recommended that LeSueur's *Catostomus duquesnii* be recognized and known as *Moxostoma duquesnii* (LeSueur). Hubbs did not rely entirely on the pelvic ray count to distinguish *duquesnei* and found that about two-thirds of *duquesnei* had 10 pelvic rays.

A series of suckers collected in the Coosa River drainage of Alabama are tentatively assigned to *M. duquesnei*. They are easily distinguished from *M. erythrurum* and have all the characters of *duquesnei* except for the pelvic ray count. Eleven specimens measuring from 92 to 215 mm standard length all had no more than 9 pelvic rays. Two specimens had the pelvic fin formula of 8-9.

Stations: 8 (1, 104); 15 (1, 110); 16 (6, 193-270); 20 (1, 67); 23 (2, 84-253); 30 (1, 129); 32 (31, 23-35); 33 (6, 96-110, and 1, 228); 35 (1, 114); 46 (1, 162).

17. *Moxostoma erythrurum* (Rafinesque)

Myxostoma euryops Jordan, 1877a: 348 (original description; Oostanaula River, Ga.); Jordan and Brayton, 1878: 54; Jordan, 1879: 115.

Myxostoma macrolepidotum duquesnii.—Jordan and Brayton, 1878: 54.

Myxostoma macrolepidotum var. *dequesnei*.—Jordan, 1878: 120.

? *Moxostoma macrolepidotum duquesnei*.—Gilbert, 1891: 153.

Moxostoma erythrurum.—Fowler, 1945: 337.

M. erythrurum was never collected with *duquesnei*. *M. duquesnei* was found at elevations between 500 and 900 feet, whereas *erythrurum* was found at elevations between 400 and 500 feet.

Stations: 14 (1, 243); 22 (1, 64); 39 (3, 220-310); 44 (2, 32-102); 49 (1, 142).

18. *Moxostoma poecilurum* (Jordan)

Moxostoma poecilurum.—Gilbert, 1891: 153 (Attalla, Ala.); Hubbs, 1930: 30 (Alabama River, Benton, Ala.; key); Scott, 1951: 31.

Unlike *M. duquesnei* and *erythrurum*, *poecilurum* seems to prefer slower streams. One of 3 collections was made in the river. All of

the fins of *poecilurum* are bright red. It is quickly distinguished from the other suckers by the presence of the black bar through the lower caudal lobe. Dusky lateral stripes are in each scale row on the back and sides.

Stations: 33 (1, 225); 36 (1, 220); 53 (1, 111).

19. *Minytrema melanops* (Rafinesque)

Erimyzon melanops.—Jordan, 1877a: 347.

Minytrema melanops.—Jordan and Brayton, 1878: 54 (waters of the Alabama); Jordan, 1879: 115; Gilbert, 1891: 154 (Oxford, Ala.); Fowler, 1945: 338; Scott, 1951: 37.

No spots on scales below axis through upper part of mouth; venter very light in color.

Stations: 26 (2, 215-320); 39 (1, 240).

20. *Erimyzon sucetta* (Lacépède)

Erimyzon sucetta.—Jordan and Brayton, 1878: 54 (Alabama Basin); Jordan, 1878: 144 (description; nomenclature); 1879: 114; Gilbert, 1891: 153 (Calera, Ala.).

Jordan and Brayton (1878) gave no locality data other than "Alabama Basin." Possibly their specimens are from the lower Alabama System near Mobile. According to Hubbs (1930), Jordan (1878) confounded *sucetta* with *oblongus*. No recent records.

21. *Erimyzon oblongus* (Mitchill)

Erimyzon oblongus.—Jordan, 1877a: 346.

No recent records from the Coosa drainage; however, this sucker is known presently from other parts of the Mobile basin.

22. *Hypentelium etowanum* (Jordan)

Catostomus nigricans var. *etowanus* Jordan, 1877a: 345 (original description; Etowah River, Ga.); 1879: 114.

Catostomus nigricans etowanus.—Jordan and Brayton, 1878: 54 (Alabama Basin; Jordan, 1878: 162.

Hypentelium etowanum.—Jordan and Brayton, 1878: 86 (listed, Alabama Basin); Hubbs, 1930: 41 (description).

? *Catostomus nigricans*.—Gilbert, 1891: 153 (Alabama Basin).

Hypentelium nigricans etowanum.—Fowler, 1945: 339.

Collected from 20 stations at elevations from 200 to 900 feet, but mostly in clear, fast running streams above 500 feet. Only 5 of 63 specimens were taken below 500 feet.

Stations: 5 (2, 70-72, and 2, 126-142); 7 (3, 37-53, and 1, 230); 9 (3, 25-27; 6, 72-86 and 8, 98-152); 10 (1, 191); 11 (1, 130); 16 (2, 80-189); 20 (1, 80); 23 (6, 19-23); 24 (1, 65); 30 (2, 22-26); 31 (3, 27-32, and 1, 75); 32 (2, 34-35); 33 (2, 175-185); 34 (1, 30, and 5, 63-96); 35 (2, 30-32); 38 (1, 75); 41 (2, 26-96); 47 (1, 80); 50 (1, 64); 53 (2, 116-123).

CYPRINIDAE—Minnows

23. *Notemigonus crysoleucas* (Mitchill)

Notemigonus americanus.—Jordan, 1877a: 344.

Notemigonus chrysoleucus.—Jordan and Brayton, 1878: 53 (Alabama Basin); Jordan, 1879: 114; Gilbert, 1891: 155 (Calera, Ala.)

Stations: 37 (7, 26-37) and 53 (1, 58).

24. *Semotilus atromaculatus* (Mitchill)

Semotilus atromaculatus.—Gilbert, 1891: 155 (Alabama Basin).

Semotilus atromaculatus thoreauianus.—Fowler, 1945: 340.

Found most abundantly in clear, fast flowing streams above 1000 feet elevation. Only 3 collections were made below 700 feet, and none was below 450 feet.

Stations: 2 (62, 25-60); 5 (4, 61-73); 7 (5, 35-54); 9 (1, 60); 23 (11, 18-28); 27 (5, 50-84); 28 (3, 73-116); 30 (1, 50); 32 (3, 20-43); 35 (6, 40-71); 37 (3, 36-39).

25. *Hybopsis amblops* Rafinesque

Nocomis amblops var. *winchelli* Jordan, 1877a: 328.

Hybopsis gracilis.—Jordan, 1877a: 333.

Ceratichthys winchelli.—Jordan and Brayton, 1878: 53 ("common in the Alabama Basin").

Ceratichthys gracilis.—Jordan, 1879: 108.

Hybopsis amblops rubrifrons.—Gilbert, 1891: 155 (Attalla and Oxford, Ala.).

? *Erinemus hyalinus*.—Fowler, 1945: 341 (color description).

This species seems to have a preference for slow moving streams.

Stations: 31 (6, 50-56); 34 (2, 51); 36 (44, 58-106); 48 (1, 60).

26. *Rhinichthys atratulus* (Hermann)

Rhinichthys obtusus.—Jordan, 1877a: 331; Jordan and Brayton, 1878: 54; Jordan, 1879: 109.

Rhinichthys atronasmus obtusus.—Jordan, 1877a: 369.

Rhinichthys atronasmus croceus.—Fowler, 1945: 342.

No new records.

27. *Phenacobius catostomus* Jordan

Phenacobius catostomus Jordan, 1877a: 332 (original description; Silver Creek, Etowah River, Ga.).—Jordan and Brayton, 1878: 53; Jordan, 1879: 109.

Not common anywhere in the Coosa drainage of Alabama.

Stations: 6 (1, 66); 14 (2, 75-80); 31 (1, 63); 33 (3, 70-83).

28. *Notropis volucellus* (Cope)

Notropis volucellus.—Howell, 1957: 56 (Little Canoe Creek, St. Clair-Etowah County line).

This species, distinguished from other *Notropis* of the Coosa drainage by the high, narrow, anterior lateral line scales, was first reported in these waters by Howell (1957).

Stations: 14 (2, 38-40); 19 (4, 50-61); 20 (1, 50); 23 (2, 52-60).

29. *Notropis venustus stigmaturus* (Jordan)

Photogenis stigmaturus Jordan, 1877a: 337 (original description; Etowah, Oostanaula and Coosa Rivers, Ga.).

Codoma stigmaturus.—Jordan and Brayton, 1878: 50.

Codoma stigmatura.—Jordan, 1879: 111.

Notropis venustus cerostigma.—Gilbert, 1891: 154 (Alabama Basin).

Notropis stigmaturus.—Fowler, 1910: 281 (Etowah R.); 1923: 20 (Rome, Ga.); 1945: 344.

Erogala stigmatura.—Fowler, 1935: 72 (Armuchee, Ga.).

Notropis venustus stigmaturus.—Gibbs, 1957: 192 (upper Alabama River; description; distribution).

This minnow was found abundantly throughout the study area.

Breeding males and gravid females were common at those stations where series were taken.

Lateral line scale counts and depth measurements of 113 specimens varied from 39 to 46 and from 18.4 to 24.5 per cent of standard length respectively. The body depth figures exceed the upper limits of 22.5 per cent of standard length given by Gibbs (1957) for *Notropis venustus stigmaturus*; however, gravid females were among the lot measured.

The following measurements are in standard lengths and to the nearest millimeter.

Stations: 15 (2, 56-64); 17 (4, 53-84); 20 (6, 49-57); 22 (20, 51-95); 23 (3, 31-54); 29 (1, 96); 30 (3, 54-77); 31 (67, 48-69); 32 (18, 32-42); 35 (1, 76); 37 (2, 60-61); 38 (3, 30-53); 44 (18, 42-78); 46 (6, 51-98); 47 (8, 47-88); 48 (1, 69); 53 (25, 47-84).

30. *Notropis callistius* (Jordan)

Photogenis callistius Jordan, 1877a: 337 (original description; Etowah and Oostanaula Rivers, Ga.)

Codoma callistius.—Jordan and Brayton, 1878: 50.

Codoma callistia.—Jordan, 1879: 111.

Notropis callistius.—Gilbert, 1891: 154 (Alabama Basin); Fowler, 1910: 281 (Etowah R.), 1945: 344; Howell, 1957: 93 (Terrapin Creek, Piedmont, Calhoun Co., Ala.).

Breeding males with well developed tubercles were observed at several stations.

Stations: 11 (1); 17 (1, 85); 20 (2, 37-40, and 1, 85); 29 (4, 44-67); 30 (2, 37-45); 46 (2, 60-65); 47 (9, 55-94).

31. *Notropis trichroistius* (Jordan and Gilbert)

Codoma trichroistia Jordan and Gilbert in Jordan and Brayton, 1878: 50 (original description; Etowah R., Rome, Ga.).—Jordan, 1879: 111.

Notropis trichroistius.—Gilbert, 1891: 154 (Alabama Basin); Fowler, 1945: 344; Howell, 1957: 102 (Little Canoe Cr.).

The tricolor shiner prefers clear, cool streams and was not collected at elevations of less than 500 feet. Breeding males were collected. The tubercles are prominent but smaller than those of *N. callistius*. The body is light steel blue above, becoming silvery below. The subcaudal spot is deep blue. The pectoral, pelvic, and caudal fins are pink. Jet black patches are found between the posterior dorsal rays. The tip of the dorsal fin is bright red and the base is deep blue-black. The tips of the anal, pelvic and pectoral fins are also bright red.

Stations: 1 (17, 35-71); 9 (36, 42-80); 16 (2, 40-56); 19 (2, 36-48); 20 (32, 27-62); 24 (4, 26-32, and 7, 40-67); 27 (1, 69); 29 (2, 27-30, and 20, 41-98); 30 (16, 36-74); 31 (21, 42-67); 34 (16, 43-73); 35 (18, 30-44, and 25, 51-76); 38 (86, 25-74).

32. *Notropis caeruleus* (Jordan)

Photogenis caeruleus Jordan, 1877a: 338 (original description; tributaries of the Oostanaula River, above Rome, Ga.),

Erogala caerulea.—Jordan and Brayton, 1878: 51 (Oostanaula River and its tributaries).

Codoma caerulea.—Jordan, 1879: 111.

Notropis coeruleus.—Gilbert, 1891: 154 (Attalla and Oxford, Ala.).

Notropis caeruleus.—Fowler, 1910: 282; 1945: 345.

This minnow, endemic to the Alabama Basin, is not common anywhere within its range. The scales of the back and sides are marked much like those of *Notropis venustus*. The ground color of the back and sides of specimens fresh from the water is light olive blue, and the lateral band is rich steel blue. The posterior end of the lateral band is only slightly expanded and little darker. The fins are light pink with few melanophores. The belly is silvery. The snout is blunter and the body deeper than other members of the subgenus *Cyprinella* listed herein.

Three specimens measuring from 50 to 80 mm were collected at station 23.

33. *Notropis asperifrons* Suttkus and Raney

Notropis asperifrons Suttkus and Raney, 1955b: 3-33 (original description; Holly Creek, Murray Co., Ga.; paratypes from the Coosa River drainage are from Cherokee, Calhoun, Talladega, and Shelby Counties, Ala., and Whitfield Co., Ga.).

Stations: 16 (1, 61); 19 (3, 50-62); 20 (2, 51-64); 22 (1, 58); 29 (24, 39-67); 31 (6, 36-55); 38 (27, 40-59); 39 (18, 38-53); 40 (2, 50-51); 44 (1, 50).

34. *Notropis baileyi* Suttkus and Raney

Notropis baileyi Suttkus and Raney, 1955a: 71-86 (original description; Sawacklahatchee Creek, Macon Co., Ala.).

Suttkus and Raney (1955a) reported a single specimen of *N. baileyi* in the Coosa River System from Etowah Co., Ala. This remains the northernmost record for the species. Fifty-five specimens collected from 5 stations in the southernmost 3 counties of the study area further verifies the presence of the species in the Coosa drainage.

Stations: 46 (17, 46-68); 47 (13, 51-60); 48 (11, 51-73); 50 (13, 30-56); 52 (1, 57).

35. *Notropis xanocephalus* (Jordan)

Hybopsis xanocephalus Jordan, 1877a: 334 (original description; Etowah, Oostanaula and Coosa Rivers, Ga.).

Hydrophlox xanocephalus.—Jordan and Brayton, 1878: 49.

Alburnops xanocephalus.—Jordan, 1879: 110.

Notropis xanocephalus.—Gilbert, 1891: 154 (Alabama Basin); Fowler, 1910: 288 (Etowah R.), 1945: 346; Howell, 1957: 162 (St. Clair and Etowah Co.).

Generally distributed throughout the Coosa drainage of Alabama, and often associated with *N. chrosomus* but rarely with *N. asperifrons*.

Stations: 7 (9, 22-47); 9 (18, 45-68); 13 (9, 21-47); 14 (6, 23-49); 23 (4, 41-46); 24 (21, 32-56); 26 (5, 50-67); 30 (33, 44-66); 34 (15, 43-64); 35 (26, 47-64); 41 (5, 53-57); 44 (1, 40).

36. *Notropis chrosomus* (Jordan)

Hybopsis chrosomus Jordan, 1877a: 333 (original description; Etowah River, Ga.).

Hydrophlox chrosomus.—Jordan and Brayton, 1878: 49.

Alburnops chrosomus.—Jordan, 1879: 110.

Notropis chrosomus.—Fowler, 1910: 287 (Etowah R.), 1945: 346; Howell, 1957: 181 (Etowah Co., Ala.).

The body of live specimens is multicolored with an iridescence of blues and reds. The almost undiscernible longitudinal alternating light and dark bands along the back and sides are obscured by the iridescence. The bases of the dorsal, anal, and pelvic fins are red. The pectoral fins are pink; the caudal fin has scattered melanophores in the central portion.

Stations: 5 (14, 44-66); 7 (12, 43-57); 16 (8, 51-64); 22 (1, 46); 24 (10, 34-60); 31 (1, 57); 34 (4, 57-70); 35 (5, 46-55); 38 (17, 46-58); 41 (1, 63); 44 (2, 46-57).

37. *Notropis cornutus* (Mitchill)

Luxilus cornutus.—Jordan, 1877a: 340; Jordan and Brayton, 1878: 49; Jordan, 1879: 110.

Notropis megalops.—Gilbert, 1891: 154 (Alabama Basin).

Notropis cornutus chrysocephalus.—Fowler, 1945: 345.

Notropis cornutus.—Howell, 1957: 193.

Especially abundant in the lower 2/3 of the Coosa drainage of Alabama.

Stations: 7 (11); 14 (2); 16 (3, 67-80, and 1, 118); 18 (1, 70); 19 (2, 33-70); 23 (1, 56); 26 (1, 103); 31 (11, 70-157); 32 (2, 82-91); 33 (2, 77-80); 34 (7, 77-123); 38 (3, 56-57); 39 (3, 63-75); 44 (1, 133); 47 (4, 64-69); 48 (14, 57-78); 50 (4, 59-71); 53 (27, 47-80).

38. *Notropis atherinoides* Rafinesque

Notropis atherinoides was reported in the Coosa River for the first time by Howell (1957). It is very similar to *N. stilbius* but may be distinguished from it by the character of the slightly more slender and compressed body and by the shorter snout. Howell pointed to the fact that *atherinoides* prefers larger streams. This observation also applied to specimens from the Coosa drainage. Of the three collections, two were made in the river proper and one in a sluggish stream only one mile from the river.

Stations: 36 (200, 30-57); 37 (5, 52-64); 51 (1, 59).

39. *Notropis stilbius* (Jordan)

Nototropis stilbius Jordan, 1877a: 343 (original description: Etowah River, Ga.).

Notropis stilbius.—Jordan and Brayton, 1878: 53 (Alabama Basin); Jordan, 1879: 111; Gilbert, 1891: 154 (Alabama Basin); Fowler, 1910: 289 (Etowah R.), 1935: 72 (Armuchee, Ga.), 1945: 349; Howell, 1957: 225 (Little Canoe Cr.).

Unlike *N. atherinoides*, *stilbius* is found in smaller streams usually at considerable distances from the river. It was collected at elevations from 400 to 600 feet.

Stations: 14 (18, 36-64); 19 (3, 52-53); 22 (16, 55-76); 31 (25, 42-69); 32 (1, 69); 33 (1, 58); 34 (1, 64); 44 (1, 73); 46 (3, 64-74); 47 (1, 58); 49 (15, 42-69).

40. *Notropis bellus* (Hay)

Breeding males and females were collected at both stations. This apparently represents the first record of the species in the Coosa River system.

Stations: 44 (10, 48-62); 52 (21, 53-69).

41. *Notropis lirus* (Jordan)

Nototropis lirus Jordan, 1877a: 342 (original description; Etowah R., Ga.).

Notropis lirus.—Jordan and Brayton, 1878: 53; Jordan, 1879: 113; Fowler, 1945: 238 (Etowah R.), 348.

Males with well developed tubercles and gravid females were collected at several stations. The smallest gravid female was 42 mm total length.

Stations: 16 (2 of 15, 47-49); 18 (6, 38-54); 19 (3, 46-52); 20 (15, 38-54); 26 (1 of 10, 55); 30 (1, 55); 31 (3 of 10, 37-55); 34 (3, 36-41); 35 (1 of 8, 53); 38 (19 of 85, 27-52); 39 (1 of 15, 40); 40 (18, 42-54).

42. *Ericymba buccata* Cope

This distinctive minnow, not previously reported from the Coosa System, was taken in 2 collections over rock, sand and gravel.

Stations: 53 (9, 35-60); 54 (2, 25-26, and 6, 41-60).

43. *Pimephales vigilax* (Baird and Girard)

Cliola vigilax.—Gilbert, 1891: 154 (Attalla, Ala.).

Lythrurus lirus.—Fowler, 1935: 72 (Armuchee, Ga.; corrected by Fowler (1945: 233) to *Ceratalichthys vigilax*).

Ceratalichthys velox.—Fowler, 1945: 342.

No new records.

44. *Pimephales notatus* (Rafinesque)

Hyborhynchus notatus.—Fowler, 1945: 340.

No new records.

45. *Campostoma anomalum* (Rafinesque)

Campostoma anomalum var. *anomalum* Jordan, 1877a: 325.

Campostoma anomalum var. *prolixum* Jordan and Brayton, 1878: 49.

Campostoma anomalum.—Jordan, 1879: 107; Gilbert, 1891: 154 (Alabama Basin); Fowler, 1935: 72 (Armuchee, Ga.).

Campostoma anomalum anomalum.—Fowler, 1945: 340.

Very abundant throughout the Coosa drainage of Alabama.

Stations: 7 (5, 32-52); 9 (5, 63-82); 14 (2, 34-82); 16 (1, 41); 19 (5, 26-31); 20 (1, 101); 22 (1, 118); 24 (2, 48-67); 25 (1, 110); 26 (1, 36); 31 (3, 29-30, and 2, 57-67); 32 (3, 26-32, and 2, 85); 33 (2, 77-80); 34 (2, 29-55); 35 (9, 20-38, and 5, 61-73); 37 (1, 35); 38 (2, 71-94); 41 (8, 18-38, and 1, 60); 53 (1, 61).

ICTALURIDAE—Catfishes

46. *Ictalurus punctatus* (Rafinesque)

Ichthaelurus punctatus.—Jordan, 1877a: 350; Jordan and Brayton, 1878: 55 (basin of the Alabama).

Ictalurus punctatus.—Gilbert, 1891: 153 (Attalla, Ala.); Fowler, 1935: 72 (Armuchee, Ga.).

- Ictalurus lacustris punctatus*.—Fowler, 1945: 350; Scott, 1951: 31.
Taken only in the river proper.
Stations: 36 (67, 40-90, and 1, 137); 43 (12, 192-230); 51 (2, 160).
47. *Ictalurus furcatus* (LeSueur)
? *Ictalurus ponderosus*.—Fowler, 1945: 350 (identification from photograph).
Ictalurus furcatus.—Scott, 1951: 31.
Six specimens measuring from 190 to 230 mm were taken in traps at station 43.
48. *Ictalurus natalis* (LeSueur)
Amiurus cupreus.—Jordan, 1877a: 351.
Amiurus lividus.—Jordan, 1877a: 368.
Amiurus natalis antoniensis.—Jordan and Brayton, 1878: 55.
Ameiurus natalis erebennus.—Fowler, 1945: 350.
No new records.
49. *Ictalurus melas* (Rafinesque)
Ameiurus melas melas.—Fowler, 1945: 350.
One specimen measuring 66 mm was collected at station 35.
50. *Pylodictis olivaris* (Rafinesque)
Pylodictis olivaris.—Scott, 1951: 31.
One specimen measuring 232 mm was collected at station 36.
51. *Noturus leptacanthus* Jordan
Noturus leptacanthus Jordan, 1877a: 352 (original description; Etowah River, Rome, Ga.).—Jordan and Brayton, 1878: 55; Jordan, 1879: 119; Gilbert, 1891: 153 (Attalla, Ala.).
Schilbeodes leptacanthus.—Fowler, 1945: 351; Scott, 1951: 37.
No new records.

ANGUILLIDAE—Freshwater Eels

52. *Anguilla rostrata* (LeSueur)
Anguilla vulgaris.—Jordan, 1877a: 352; Jordan and Brayton, 1878: 55 (Alabama Basin); Jordan, 1879: 119.
One specimen measuring 315 mm was collected at station 51.

AMBLYOPSIDAE—Cave Fishes

53. *Typhlichthys subterraneus* Girard
A series of 10 specimens collected at station 4 is tentatively assigned to this species. This constitutes the first record of the genus in the Mobile basin.

CYPRINODONTIDAE—Topminnows

54. *Fundulus stellifer* (Jordan)
Xenisma stellifer Jordan, 1877a: 322 (original description; Etowah, Oostanaula and Coosa Rivers, near Rome, Ga.).
Xenisma stelliferum.—Jordan and Brayton, 1878: 48; Jordan, 1879: 103.
Fundulus stellifer.—Gilbert, 1891: 155 (Attalla and Oxford, Ala.); Fowler, 1945: 352.

This minnow, endemic to the Coosa River system of Alabama and Georgia, is one of the most colorful of freshwater cyprinodont

fishes. Adult males, fresh from the water, have an iridescence dominated by greenish-blue. Bright red specks are present over most of the body, head, dorsal fin, and base of anal fin. The red specks usually form irregularly broken lateral stripes. The dorsal, caudal, anal, and pelvic fins are pale pinkish; the pectorals are practically clear. Most striking in adult males is the jet black band bordering the dorsal and caudal fins.

The females and young males are less colorful. The ground color is light olive; the fins are very pale, except for the dorsal and caudal which are light straw color. Most of the head and body are covered with olive-black specks. The belly is silvery.

Females with mature eggs were observed at several stations.

Stations: 7 (8, 50-67); 16 (1, 51, and 5, 88-105); 23 (1, 91); 24 (7, 47-83); 30 (1, 37, and 2, 85-95); 31 (15, 45-96); 35 (4, 60-81).

55. *Fundulus notatus* (Rafinesque)

Fundulus notatus.—Fowler, 1945: 352.

Brown (1956) listed *Fundulus olivaceus* from the Alabama River and *F. notatus* from the Tombigbee River, Alabama. Our Coosa River specimens are tentatively assigned to *F. notatus* until an analysis of the Mobile basin *notatus-olivaceus* complex is completed. The modal number of dorsal and anal rays is 10 and 12, respectively. The mean is 9.6 and 11.8, respectively. We recognize sexual dimorphism, as well as a high degree of color pattern variation within sexes. Several females were heavy with mature eggs.

Stations: 15 (2, 52-60); 16 (4, 45-61); 18 (2, 50-64); 22 (2, 60-63); 31 (13, 40-67); 40 (1, 69); 42 (2, 58-61); 44 (2, 51-58); 51 (1, 62); 52 (5, 51-72); 53 (3, 45-64).

56. *Gambusia affinis* (Baird and Girard)

Gambusia patruelis.—Fowler, 1945: 352.

The ratio of males to females was 1: 6. Many of the females were heavy with young.

Stations: 12 (4 females, 32-50); 18 (1 female, 37); 19 (7 females, 35-49); 23 (27 females, 15-45, and 8 males, 22-28); 26 (18 females, 19-51, and 2 males, 30-31); 29 (2 females, 40); 37 (5 females, 37-43, and 1 male, 23); 38 (1 female, 40).

APHREDODERIDAE—Pirate Perches

57. *Aphredoderus sayanus* (Gilliams)

Aphododerus sayanus. Jordan, 1877a: 368 (listed; Coosa R.); Jordan and Brayton, 1878: 47 (Alabama River, Montgomery, Ala.).

No recent records.

MUGILIDAE—Mulletts

58. *Mugil cephalus* Linnaeus

Mugil cephalus.—Byrd, 1954: 3 (Coosa River near Wetumpka, Ala.);

Boschung and Hemphill, 1960: 73 (distribution in fresh water).

Two specimens measuring approximately 250 mm were found dead on the beach at station 51. Striped Mullet have been observed in the Cahaba and Coosa Rivers in Alabama for several years. They are caught on hook and line using earthworms for bait.

SERRANIDAE—Basses

59. *Roccus saxatilis* (Walbaum)

Roccus striatus.—Bean, 1884: 242 (Montgomery, Ala.).

Concerning *Roccus saxatilis*, I. B. Byrd, Chief Biologist, Fisheries Section, Alabama Department of Conservation, stated, "Peak runs of saltwater striped bass up the Coosa to Jordan Dam and up the Tallapoosa to Tallassee Dam occur each year during May and June. Hundreds of fishermen fish below these two dams—particularly below the Tallassee Dam for the stripes. Specimens of 10 to 25 pounds are commonly caught. One 55-pounder was taken last year below Tallassee Dam."

60. *Roccus chrysops* (Rafinesque)

Lepibema chrysops.—Scott, 1951: 31.

Two specimens measuring 130 and 140 mm were collected at station 36.

CENTRARCHIDAE—Sunfishes

61. *Micropterus punctulatus henshalli* Hubbs and Bailey

Micropterus punctulatus henshalli.—Fowler, 1945: 361; Scott, 1951: 31.

Micropterus pallidus (in part).—Jordan, 1877a: 314; Jordan and Brayton, 1878: 46; Jordan, 1879: 100.

Micropterus pseudaplites (in part).—Hubbs, 1927: 13 (Rome, Ga.).

Stations: 14 (2, 40-106); 22 (2, 84-98); 45 (2, 49-108); 51 (1, 43).

62. *Micropterus coosae* Hubbs and Bailey

Micropterus coosae Hubbs and Bailey, 1940: 23 (original description:

Big Will's Creek, Etowah Co., Ala.).—Fowler, 1945: 361.

Micropterus salmoides (in part).—Jordan, 1877a: 314.

Micropterus salmoides var. *salmoides*.—Jordan and Brayton, 1878: 46 (Alabama Basin).

Micropterus pseudaplites (in part).—Hubbs, 1927: 13 (Rome, Ga.).

Stations: 3 (1, 136); 5 (1, 88); 9 (2, 74-84); 24 (1, 59); 37 (1, 113); 39 (1, 241); 53 (1, 108).

63. *Micropterus salmoides* (Lacépède)

Micropterus salmoides (in part).—Jordan, 1877a: 314; Jordan and Brayton, 1878: 46 (Alabama Basin); Jordan, 1879: 100; Gilbert, 1891: 155 (Alabama Basin).

Micropterus pallidus (in part).—Jordan, 1877a: 314.

M. salmoides, the largemouth black bass, seems to be more common in the Coosa River drainage of Alabama than the preceding two species of the genus *Micropterus*.

- Stations*: 23 (3, 26-40; 1, 97, and 1, 310); 28 (2, 98-100); 31 (1, 37); 32 (4, 22-59); 36 (3, 135-197); 37 (1, 152); 42 (4, 43-48); 44 (1, 166); 52 (1, 51); 53 (2, 58-143).
64. *Chaenobryttus gulosus* (Cuvier)
Chaenobryttus gulosus.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 46 (Alabama River, Montgomery, Ala.).
Chaenobryttus coronarius.—Scott, 1951: 31.
Stations: 9 (1, 115); 23 (1, 140); 39 (1, 110).
65. *Lepomis cyanellus* Rafinesque
Lepomis cyanellus.—Scott, 1951: 31.
Stations: 27 (14, 53-108); 28 (1, 65); 29 (1, 36); 35 (2, 60-68); 54 (4, 66-80).
66. *Lepomis microlophus* (Günther)
Twelve specimens from 5 stations are referable to this species. These constitute what are apparently the first records of the species from the Coosa River System.
Stations: 15 (1, 125); 18 (3, 63-74); 29 (5, 43-74); 42 (2, 72-125); 51 (1, 142).
67. *Lepomis megalotis* (Rafinesque)
Xenotis sanguinolentus.—Jordan, 1877a: 318; Jordan and Brayton, 1878: 46; Jordan, 1879: 98.
Xenotis inscriptus.—Jordan, 1877a: 318, 1877b: 42 (Etowah R.); Jordan and Brayton, 1878: 46.
Lepomis megalotis megalotis.—Gilbert, 1891: 155 (Alabama Basin); Fowler, 1945: 360; Scott, 1951: 31.
Abundant throughout the area.
Stations: 2 (4, 40-55); 8 (1, 103); 13 (5, 66-92); 14 (3, 37-71); 18 (1, 66); 19 (1, 38); 22 (3, 44-45); 31 (5, 45-95); 32 (2, 62-70); 33 (2, 122-129); 37 (2, 67-75); 39 (4, 33-51); 40 (3, 33-41); 44 (1, 64); 45 (1, 38); 52 (4, 60-90); 53 (4, 41-73).
68. *Lepomis macrochirus* Rafinesque
Lepiopus obscurus.—Jordan, 1877a: 317 (description); Jordan and Brayton, 1878: 46; Jordan, 1879: 99.
Lepiopus pallidus.—Jordan, 1877a: 316; Jordan and Brayton, 1878: 46; Jordan, 1879: 99.
Helioperca obscura.—1877a: 369 (listed).
? *Helioperca pallida*.—Jordan, 1877a: 369 (listed).
? *Eupomotis pallidus*.—Jordan, 1877a: 368 (listed); 1877b: 21 (Alabama River).
Lepomis macrochira macrochira.—Fowler, 1945: 360.
Lepomis macrochirus macrochirus.—Scott, 1951: 31.
Abundant throughout the area.
Stations: 8 (2, 50-77); 13 (1, 85); 14 (7, 42-104); 15 (2, 56-78); 16 (3, 45-50); 17 (1, 35); 18 (2, 41-60); 19 (2, 40-75); 20 (1, 65); 22 (7, 45-72); 28 (1, 44); 29 (4, 30-55); 30 (13, 28-46); 31 (14, 29-37, and 1, 161); 33 (1, 165); 37 (3, 24-27, and 1, 65); 39 (1, 52); 41 (1, 58); 42 (4, 47-98); 49 (1, 67); 51 (2, 72-85); 53 (6, 37-48).

69. *Ambloplites rupestris* (Rafinesque)
Ambloplites rupestris.—Jordan, 1877a: 316; Jordan and Brayton, 1878: 46; Jordan, 1879: 100.
Ambloplites rupestris rupestris.—Scott, 1951: 37.
 No new records.
70. *Pomoxis nigromaculatus* (LeSueur)
Pomoxys hexacanthus.—Jordan, 1877a: 368.
 One specimen measuring 111 mm was collected at station 23.
71. *Pomoxis annularis* Rafinesque
Pomoxys annularis.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 47 (Round Lake, Montgomery, Ala.).
Pomoxis annularis.—Scott, 1951: 31.
 One specimen measuring 95 mm was collected at station 18.
72. *Centrarchus macropterus* (Lacépède)
Centrarchus irideus.—Jordan, 1877a: 368; Jordan and Brayton, 1878: 47 (Alabama River, Montgomery, Ala.).
 No recent records. This species is known presently from the Warrior River drainage of the Mobile basin.

PERCIDAE—Perches

73. *Stizostedion vitreum* (Mitchill)
Stizostethium salmoneum.—Jordan, 1877a: 313; Jordan and Brayton, 1878: 45; Jordan, 1879: 96.
Stizostedion vitreum vitreum.—Fowler, 1945: 352; Scott, 1951: 37.
 No new records.
74. *Percina caprodes* (Rafinesque)
Percina caprodes.—Jordan, 1877a: 312; Jordan and Brayton, 1878: 45 (Alabama River).
Etheostoma caprodes.—Gilbert, 1891: 155 (Alabama Basin).
Percina caprodes caprodes.—Fowler, 1945: 354.
 Stations: 6 (3, 112-116); 21 (1, 85); 33 (1, 90); 38 (4, 70-102); 39 (1, 99); 40 (1, 107); 42 (5, 48-97); 44 (1, 123); 47 (1, 105); 49 (2, 95-107); 52 (1, 90).
75. *Percina nigrofasciata* (Agassiz)
Hadropterus nigrofasciatus.—Jordan, 1877a: 310; Jordan and Brayton, 1878: 45 (Alabama Basin); Jordan, 1879: 96.
Etheostoma nigrofasciatum.—Gilbert, 1891: 155 (Alabama Basin).
Hadropterus nigrofasciatus nigrofasciatus.—Fowler, 1945: 354.
Percina nigrofasciata nigrofasciata.—Crawford, 1956: 8 (records from the Coosa River drainage of Alabama and Georgia; description).
 Stations: 9 (5, 63-82); 22 (3, 43-70); 26 (9, 47-93); 38 (1, 61).
76. *Percina palmaris* (Bailey)
Hadropterus palmaris Bailey, 1940: 524-580 (original description; Etowah River, Lumpkin Co., Ga.).—Crawford, 1954: 235 (tributaries of the Etowah River, Ga., and Cherokee-Calhoun Co. line, Ala.).
 Crawford (1954) listed a collection "Cornell University . . . No. 21158, Cherokee-Calhoun Co. line on Rte. 74, Ga." Undoubtedly Crawford intended to list the record from Alabama. Cherokee County, Alabama is adjacent to Calhoun County, and Route 74 is an Alabama State highway and also U.S. highway 278.
 One specimen measuring 67 mm was collected at station 48.

77. *Ammocrypta asprella* (Jordan)
Pleurolepis asprellus.—Jordan and Brayton, 1878: 82 (Montgomery, Ala.).
Etheostoma asprellum.—Gilbert, 1891: 155 (Oxford, Ala.).
No recent records.
78. *Etheostoma stigmaeum* (Jordan)
Boleosoma stigmaeum Jordan, 1877a: 307 (original description; Etowah and Oostanaula Rivers, Ga.).
Ulocentra stigmaea.—Jordan and Brayton, 1878: 45 (Alabama Basin); Fowler, 1945: 354.
Etheostoma stigmaeum.—Gilbert, 1891: 155 (Alabama Basin).
Stations: 6 (1, 48); 7 (1, 48); 9 (1, 54); 31 (3, 40-43); 34 (5, 35-46); 35 (3, 45-53); 37 (3, 51-53); 38 (1, 43).
79. *Etheostoma blennioides* Rafinesque
Etheostoma blennioides.—Fowler, 1945: 355.
No new records.
80. *Etheostoma coosae* (Fowler)
Poecilichthys coosae Fowler, 1945: 356 (original description; Coosa River, Cherokee Co., Ala.).
Etheostoma (Ulocentra) coosae.—Bailey and Gosline, 1955: 40 (listed, Floyd and Polk Co., Ga., and Etowah Co., Ala.).
No new records.
81. *Etheostoma (Ulocentra)* sp.
This undescribed species is represented by 34 specimens.
Stations: 5 (3); 7 (6); 9 (4); 13 (4); 14 (1); 16 (1); 24 (7); 35 (1); 38 (6); 44 (1).
82. *Etheostoma jordani* Gilbert
Etheostoma (Nothonotus) jordani Gilbert, 1891: 156 (original description; Choccolo Creek, Oxford, and Chestnut Creek, Verbena, Ala.).—Bailey and Gosline, 1955: 40 (listed, Whitfield Co., Ga.).
One specimen measuring 53 mm was collected at station 36.
83. *Etheostoma whipplei; artesia* (Hay)
Three specimens measuring from 44 to 49 mm were collected at station 40. Although this species is known from the Warrior drainage, these specimens apparently constitute the first records of the species from the Coosa.

SCIAENIDAE—Drums

84. *Aplodinotus grunniens* Rafinesque
Haploidonotus grunniens.—Jordan, 1877a: 319; Jordan and Brayton, 1878: 47; Jordan, 1879: 101.
Aplodinotus grunniens.—Scott, 1951: 31.
Three specimens measuring from 81 to 90 mm were collected at station 36.

COTTIDAE—Sculpins

85. *Cottus carolinae* (Gill)
Potamocottus zopherus Jordan, 1877a: 320 (original description; Etowah and Oostanaula Rivers, Ga.); 1879: 102.
Potamocottus meridionalis.—Jordan and Brayton, 1878: 47.

Cottus bairdi.—Gilbert, 1891: 157 (Attalla and Oxford, Ala.).

? *Cottus bairdii bairdii*.—Fowler, 1945: 362.

Stations: 6 (53, 22-68); 7 (1, 63); 22 (3, 23-25); 23 (1, 26); 26 (1, 28); 29 (1, 22); 35 (2, 25-55); 38 (2, 25-29); 41 (1, 32).

SPECIES OF DOUBTFUL OCCURRENCE

The following species have been reported from the Coosa River system by previous authors, but their occurrence there seems doubtful.

86. *Semotilus corporalis* (Mitchill)

Semotilus corporalis.—Jordan, 1877a: 327; Jordan and Brayton, 1878: 54; Jordan, 1879: 107.

87. *Notropis rubricroceus* (Cope)

Notropis rubricroceus.—Fowler, 1945: 345.

88. *Notropis photogenis* (Cope)

Notropis photogenis.—Fowler, 1945: 349.

89. *Etheostoma simoterum* (Cope)

Etheostoma simoterum.—Gilbert, 1891: 155 (Alabama Basin).

90. *Boleichthys elegans* Girard

Boleichthys elegans.—Jordan, 1877a: 308; Jordan and Brayton, 1878: 45 (Alabama Basin); Jordan, 1879: 94.

91. *Etheostoma squamiceps* Jordan

Etheostoma squamiceps.—Gilbert, 1891: 156 (Calera, Ala.).

DISTRIBUTION

Ten species (*Hypentelium etowanum*, *Notropis callistius* N. *trichroistius*, *N. caeruleus*, *N. xanocephalus*, *N. chrosomus*, *Fundulus stellifer*, *Percina palmaris*, *Etheostoma coosae*, and *E. jordani*) and possibly the undescribed *Etheostomid* of the subgenus *Ulocentra* are endemic to the upper Alabama system. *Notropis asperifrons* and *N. venustus stigmatatus* of the Coosa fauna are limited to the Mobile basin. *Notropis baileyi*, *N. stilbius*, *N. bellus*, *Noturus leptacanthus*, and *Micropterus coosae* are Coosa fishes that are also found in two or more Gulf drainages east of the Mississippi. It is probable that they originated in the Mobile basin. *Phenacobius catostomus* and *Notropis lirus* are shared by the Coosa and Tennessee systems and probably originated in the latter.

Two (*Mugil cephalus* and *Roccus saxatilis*) are marine forms which migrate upstream to the base of Jordan Dam. The dam also serves as a barrier to further upstream migration of the euryhaline shad, *Alosa chrysochloris*. *Anguilla rostrata*, historically known from the Etowah and Oostanaula Rivers of Georgia (Jordan, 1877a), and *Ericymba buccata* were not collected in the Coosa above Jordan Dam. *Dorosoma petenense* is represented in the lakes by residual populations. In addition to these species, *Ictiobus bubalus*, *Notropis atherinoides*, *N. bellus*, *Pylodictis olivaris*, *Roccus chrysops*, and *Etheostoma whipplei artesiae* are not known in the Coosa drainage above station 36 (Fig. 1).

Excluding the 6 species of doubtful occurrence, the fish fauna of the Coosa River drainage of Georgia and Alabama comprise 20 families and 85 species. Ten (*Polyodon spathula*, *Alosa chrysochloris*, *Dorosoma petenense*, *Notropis volucellus*, *N. atherinoides*, *N. bellus*,

Ericymba buccata, *Typhlichthys subterraneus*, *Lepomis microlophus*, and *Etheostoma whipplei artesiæ*) are reported herein from the Coosa drainage for the first time.

CLASSIFICATION OF THE FISHES OF THE COOSA DRAINAGE OF ALABAMA
BASED ON HABITAT PREFERENCES

I. Species limited to streams and tributaries.

<i>Ichthyomyzon gagei</i>	<i>Notropis lirus</i>
<i>Esox americanus</i>	<i>Ericymba buccata</i>
<i>Esox niger</i>	<i>Pimephales vigilax</i>
<i>Moxostoma erythrurum</i>	<i>Pimephales notatus</i>
<i>Hypentelium etowanum</i>	<i>Campostoma anomalum</i>
<i>Notemigonus crysoleucas</i>	<i>Ictalurus natalis</i> ¹
<i>Semotilus atromaculatus</i>	<i>Ictalurus melas</i> ¹
<i>Rhinichthys atratulus</i>	<i>Fundulus stellifer</i>
<i>Phenacobius catostomus</i>	<i>Gambusia affinis</i>
<i>Notropis volucellus</i>	<i>Micropterus coosae</i> ¹
<i>Notropis venustus stigmaturus</i>	<i>Chaenobryttus gulosus</i> ¹
<i>Notropis callistius</i>	<i>Pomoxis nigromaculatus</i> ¹
<i>Notropis trichroistius</i>	<i>Percina nigrofasciata</i>
<i>Notropis caeruleus</i>	<i>Percina palmaris</i>
<i>Notropis asperifrons</i>	<i>Ammocrypta asprella</i>
<i>Notropis baileyi</i>	<i>Etheostoma stigmaeum</i>
<i>Notropis xanoecephalus</i>	<i>Etheostoma blennioides</i>
<i>Notropis chrosomus</i>	<i>Etheostoma coosae</i>
<i>Notropis cornutus</i>	<i>Etheostoma (Ulocentra) sp.</i>
<i>Notropis stilbius</i>	<i>Etheostoma whipplei artesiæ</i>
<i>Notropis bellus</i>	<i>Cottus carolinæ</i>

II. Species limited to the river and the impounded waters.

<i>Polyodon spathula</i>	<i>Ictalurus punctatus</i>
<i>Acipenser fulvescens</i>	<i>Ictalurus furcatus</i>
<i>Lepisosteus osseus</i>	<i>Pylodictis olivaris</i>
<i>Alosa chrysochloris</i>	<i>Anguilla rostrata</i>
<i>Dorosoma cepedianum</i>	<i>Mugil cephalus</i>
<i>Dorosoma petenense</i>	<i>Roccus saxatilis</i>
<i>Hiodon tergisus</i>	<i>Roccus chrysops</i>
<i>Cycleptus elongatus</i>	<i>Aplodinotus grunniens</i>
<i>Ictiobus bubalus</i>	

III. Species known to occur in both the river and the tributaries.

<i>Moxostoma poecilurum</i>	<i>Lepomis microlophus</i>
<i>Minytrema melanops</i>	<i>Lepomis megalotis</i>
<i>Hybopsis amblops</i>	<i>Lepomis macrochirus</i>
<i>Notropis atherinoides</i>	<i>Ambloplites rupestris</i>
<i>Noturus leptacanthus</i>	<i>Pomoxis annularis</i>
<i>Fundulus notatus</i>	<i>Stizostedion vitreum</i>
<i>Micropterus punctulatus henshalli</i>	<i>Percina caprodes</i>
<i>Micropterus salmoides</i>	<i>Etheostoma jordani</i>
<i>Lepomis cyanellus</i>	

IV. Species found in caves.

<i>Typhlichthys subterraneus</i>	<i>Cottus carolinæ</i>
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¹ Probably also belong in group II.

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Phenology of Sumacs¹

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ABSTRACT: The nature and extent of phenological variability among individuals of sumac, *Rhus glabra*, was investigated.

The phenological events considered are: bud elongation, bud opening, leaf appearance, cessation of leaf and twig growth, inflorescence appearance, first flower and fruit, and cessation of inflorescence growth. The sex of the clone, height of the stem above ground, age of the stem, and the final twig length showed association with phenological events.

Phenological stages are grouped into the cessation events which develop slowly throughout the clone, and the developmental events which occur rapidly throughout the clone.

Through the use of a multiple range test, the mean values of all clones for each event can be grouped into those which show no statistical difference from each other. The number of times one clone is grouped with another may be considered an index of the phenological similarity of the clones.

The major conclusions drawn are: (1) the phenological variability appears to be primarily associated with the genetic constitution of the plant; (2) aspects of the structure and life history of the clone seem associated to a lesser extent with its phenology; (3) exposure of the clone on the hilltop and exposure of the stem within the clone seem to have no effect on the phenology.

INTRODUCTION

There is often a difference in the time of appearance of developmental stages of different species and of different individuals of a species. Plant phenology is the study of the responses of plants to periodic changes in their environment. Though many observations have been made on the date of occurrence of certain events in the life of a plant, such as, leafing, flowering, maturation of fruit, acquisition of autumn color, or leaf-fall, there have been few studies directed toward an understanding of the extent and causes of such intraspecific variability.

An attempt has been made in this study to describe the phenological variability of two sumacs, *Rhus glabra* and *Rhus typhina*, and to understand the causes of this variability. These species were chosen for three reasons: prevalence in Washtenaw County, Michigan, short stature, and their clonal habit. The common occurrence made it possible to find suitable material with some degree of ease, whereas, their usual short stature enables detailed observations to be made on all parts of the plant. The clonal habit of growth, spreading under-

¹ I am indebted to Dr. Stanley A. Cain for his advice and encouragement throughout the course of this study. The statistical assistance of Dr. Don W. Hayne is much appreciated, and financial assistance from the Botanical Gardens of the University of Michigan and from the Graduate Student Research Fund of the Horace H. Rackham School of Graduate Studies made this work possible.

ground from one original plant, gives the same genetic constitution, with the exception of possible bud sports, to many stems covering a large area.

Preliminary studies were carried out on 48 clones of *Rhus*, 18 of which were classified as *Rhus typhina*, 6 as *Rhus glabra*, and 24 as intermediates between them. The sites of clonal growth were chosen to represent as wide an environmental variety as possible. The results of observations on the occurrence of eight phenological stages show that variation does exist in the phenology of *Rhus*. The three taxonomic groups, *Rhus glabra*, *Rhus typhina*, and the intermediate *Rhus*, exhibited responses which were much alike. Analyses of variance suggested that there might be an association between the site and some of the phenological events. Possible association between the growth of sumac and rainfall or temperature was so faint as to suggest that microclimatic studies would be necessary for further study.

During the following season, detailed observations were centered upon nine clones of *Rhus* which appeared very similar morphologically. Seven clones were carpellate, and two were staminate. All had little or no pubescence on the twigs, and the carpellate clones showed only clavate or cigar-shaped hairs on the fruit. The clones were thus considered to be *Rhus glabra*, in a wide sense, or in a strict sense, an intermediate *Rhus*, but very close to *Rhus glabra*.

The nine clones chosen for observation were considered distinct entities by virtue of physical separation from other clones and by morphological characters (chiefly pubescence of the twigs and fruits, branching angles, and height of the stem) which made for ready recognition of each clone. The clones were located on the top and on the north, south, and west flanks of a hill in the northwest portion of Washtenaw County, Michigan.

METHODS

Preparation for field work.—A topographic map with five-foot interval contour lines served as the base for the selection of sample areas within the nine clones. Reference stakes were set out in each clone and added to the map by triangulation and by measurement. Each clone was then mapped about its reference points, and the map was transferred to squared paper on which the contour lines were drawn. The scale of the map was such that each square of 3/16 inch represented one square meter. In addition to the outline of the clone, the height of the stems was added to the map as isochores of stem height. The clone was divided into four sectors centered on the tallest portion of the clone by north, south, east, and west radii. A sample section of the clone was designated by lines representing topography, height of stem, and exposure within the clone. The number of sample sections varied from 6 to 21 with variation in height and topography. The squares within each sample section were numbered, and, with a table of random numbers, one square was selected as the sample area.

Each sample area was located in the field by reference to the stakes. Within an area three sample stems were selected, using a table of random numbers. One sample twig of the previous year's growth was selected, again by using a table of random numbers. In this manner three sample twigs on three different sample stems were tagged in each sample section of each clone. The descriptions of the clones are summarized in Table I.

Phenological field methods.—Measurements were made of the dormant buds on each tagged twig, and the twig was observed on alternate days until the buds began to elongate. The bud which elongated most rapidly was tagged for future study, and measurements were made on alternate days until daily growth increments increased to more than one millimeter.

The date on which the bud was first observed to lengthen was termed "bud elongation" and is the first event recorded in the phenological summary, Table II. As the bud lengthened, the leaves first elongated with the bud and gradually bent off at an angle from the mass of the bud. When a leaf bent away from the main portion of the bud so that the tip of the leaf was separated from the main portion, the date was noted and the event was called "bud opening." This leaf was tagged and observed at subsequent visits. With further lengthening of the bud, other leaves became distinct until it was possible to see the new twig within the bud. The day on which this occurred was recorded as "leaf appearance" in the phenological summary. When the twig became visible, measurements were no longer made of the length of the bud. After leaf appearance, the length of the leaf was recorded. The length of the twig, from the base of the original bud to the base of the young leaves which mask the growing tip, was also noted. When the inflorescence appeared, measurements of the twig were made to the base of the first branch of the inflorescence. The day upon which it was possible to see the young inflorescence in the field was recorded as "inflorescence appearance." When it was possible to look into a flower, the date was noted as "first flower." The date of the first fruit was more subjective, since the swelling of the ovary was so gradual. In some flowers, the fruit hairs were easily seen to develop, and sometimes these hairs acquired a brilliant red color while the ovary was scarcely enlarged. In other fruits, however, the hairs of the fruit remained colorless for a longer period. The date of the "first fruit" was considered to occur when the ovary showed an apparent increase in size.

Measurements were made of the lengths of the leaf, twig, and inflorescence on each day during the season of rapid growth. When one measurement had remained similar for six days, the organ was not measured again until several days later. When the measurements had remained similar for 18 days (in the case of twigs and leaves) or for 10 days (in the case of inflorescences), growth of that organ was considered to have ceased and measurements were discontinued. The first day on which the final length was recorded was noted as

the day of cessation of growth in length of the twig, leaf, or inflorescence. (For the sake of brevity, the cessation of growth in length of the twig will be referred to as "twig cessation," and similarly, "leaf cessation" and "inflorescence cessation.")

TABLE I.—Descriptions of clones

Clone	Sex	Location on hill	Age of sample stems (yrs)	Sample stem height (m)	No. of sample sections	Clone extent (m)
A	F	SW slope	2-10	0.4-2.0	18	25 x 40
B	F	SE slope	4-13	0.4-2.0	21	30 x 30
C	F	Hilltop	1-13	0.4-2.5	16	24 x 25
D	F	Hilltop	4-13	1.1-3.0	8	17 x 25
E	F	NE slope	4-13	0.4-2.0	11	15 x 16
F	F	NW slope	5-11	0.4-2.5	13	13 x 17
G	F	W slope	3-11	0.4-2.5	14	20 x 20
H	M	W slope	4-9	0.4-1.5	6	15 x 15
I	M	Hilltop	2-11	0.4-2.0	15	28 x 36

TABLE II.—Phenological summary

Clone	Dates	Range	Mean	Standard Deviation
		No. of days		
Bud Elongation				
A	4/26-5/12	17	5/1	4.04
B	4/26-5/16	21	5/4	6.04
C	4/26-5/28	33	5/2	6.57
D	4/28-5/20	23	5/1	3.00
E	4/28-5/13	16	5/2	4.02
F	4/28-5/31	34	5/1	3.92
G	4/28-5/6	9	4/30	2.68
H	4/28-5/2	5	4/29	1.88
I	4/28-5/14	17	5/6	4.59
Bud Opening				
A	5/12-5/18	7	5/14	1.79
B	5/12-5/18	7	5/15	1.63
C	5/10-6/5	27	5/15	4.62
D	5/12-5/17	6	5/14	1.39
E	5/13-5/17	5	5/14	1.00
F	5/13-5/28	16	5/16	2.46
G	5/13-5/17	5	5/15	0.29
H	5/14-5/18	5	5/15	1.21
I	5/13-5/23	11	5/16	1.63
Leaf Appearance				
A	5/12-5/30	19	5/16	2.79
B	5/13-5/21	9	5/17	1.68
C	5/12-5/31	20	5/16	4.37
D	5/15-5/20	6	5/16	1.17

TABLE II.—(continued)

Clone	Dates	Range No. of days	Mean	Standard Deviation
E	5/15-5/20	6	5/16	1.11
F	5/15-5/31	17	5/18	2.74
G	5/16-5/20	5	5/17	1.10
H	5/16-5/17	2	5/16	0.29
I	5/14-5/21	8	5/17	1.49
Cessation of Leaf Growth				
A	5/23-6/20	29	6/8	7.60
B	5/26-7/9	45	6/14	9.72
C	5/30-7/1	33	6/10	9.27
D	6/4-6/27	24	6/14	7.19
E	5/21-7/10	51	6/9	8.44
F	6/5-7/1	27	6/14	7.51
G	6/3-7/4	32	6/13	8.39
H	5/28-6/21	25	6/7	6.48
I	5/25-7/9	46	6/13	9.97
Cessation of Twig Growth				
A	6/9-7/4	26	6/20	6.63
B	5/22-7/4	44	6/18	7.07
C	6/7-6/28	22	6/19	6.72
D	5/18-7/11	55	6/15	14.13
E	6/1-7/3	33	6/18	7.37
F	5/28-7/13	47	6/20	7.78
G	6/2-7/5	34	6/17	7.17
H	6/14-7/6	23	6/23	7.47
I	6/2-7/3	32	6/21	5.91
Inflorescence Appearance				
A	5/25-6/5	12	5/30	2.34
B	5/22-6/1	11	5/30	2.09
C	5/23-6/18	27	5/31	6.93
D	5/27-6/4	9	5/31	2.28
E	5/23-6/6	15	5/31	2.88
F	5/30-6/8	10	6/1	2.04
G	5/27-6/11	16	6/1	2.74
H	5/24-6/2	10	5/29	2.20
I	5/23-6/1	10	5/28	2.57
First Flower				
A	7/1-7/9	9	7/4	1.73
B	6/27-7/7	11	7/3	2.09
C	6/27-7/13	17	7/2	4.08
D	7/2-7/6	5	7/4	1.23
E	7/1-7/6	6	7/3	1.21
F	7/1-7/9	9	7/3	1.53
G	7/1-7/6	6	7/3	1.16
H	6/30-7/3	4	7/2	1.00
I	6/26-7/7	12	7/1	1.87

TABLE II.—(continued)

Clone	Dates	Range	Mean	Standard Deviation
		No. of days		
First Fruit				
A	7/6-7/12	7	7/10	1.42
B	7/6-7/11	6	7/9	1.61
C	7/2-7/19	18	7/8	4.41
D	7/9-7/15	7	7/12	2.03
E	7/8-7/10	3	7/9	0.34
F	7/5-7/11	7	7/8	1.56
G	7/8-7/13	6	7/10	1.29
H	(male)			
I	(male)			
Cessation of Inflorescence Growth				
A	6/18-7/15	28	7/2	5.66
B	6/19-7/12	24	6/28	4.89
C	6/25-7/19	25	7/5	6.61
D	6/28-7/13	16	7/3	4.68
E	6/21-7/19	29	7/5	7.01
F	6/19-7/11	23	7/1	4.85
G	6/22-7/19	28	7/9	8.75
H	6/27-7/13	17	7/4	3.84
I	6/26-7/11	16	7/3	2.93

RESULTS

The dates of nine phenological events are recorded in Table II.

The raw phenological data consist of daily records of the length of the selected twigs, leaves, and inflorescences and of notes of the dates of opening of the bud and the appearance of the leaf, the inflorescence, the first flower, and the first fruit. The complete data are held by the writer and may be consulted.

The first event of the season, bud elongation, took place over a period of from five days in clone H to 34 days in clone F. The average date of bud elongation varied from April 29th in clone H to May 6th in clone I.

Bud opening followed shortly after the initiation of growth in length, and usually all sample twigs in one clone opened within a period of a few days. The buds of the sample twigs of clones E, G, and H opened in five days, but buds of clone C opened over a period of 27 days. The average date of bud opening was from May 14th to 16th, a relatively short span of time.

Leaf appearance in clone H took place on two days, whereas all leaves studied in clone C required 20 days for appearance. The average dates of leaf appearance exhibit a range of only three days, from May 16th through May 18th. The earliest average date is May 16th and the latest May 18th.

Cessation of leaf growth occupied a much longer time in each clone, from 24 days in clone D to 51 days in clone E. The average date of cessation of leaf growth ranged from June 7th in clone H to June 14th in clones B, D, and F.

Cessation of twig growth also occurred over a long period of time; in clone C, 22 days, and in clone D, 55 days. The average dates of cessation of twig growth occurred over only eight days, from June 15th in clone D to June 23rd in clone H.

Appearance of the inflorescence on all sample twigs occurred in clone D in nine days and in clone C in 27 days. The average date of inflorescence appearance ranged from May 28th in clone I to June 1st in clones F and G.

The appearance of the first flower occurred in a relatively short time, from a range of four days in clone H to 17 days in clone C. The average dates are close together, from the 1st of July in clone I to the 4th of July in clones A and D.

The seven carpellate clones set fruit within a relatively brief period of from three days in clone E to 18 days in clone C. The earliest average date of appearance of the first fruit was July 8th in clones C and F, and the latest average date was July 12th in clone D.

The cessation of inflorescence growth, like the cessation of growth of the leaf and the twig, covered a longer period of time. Clone D exhibited the shortest range with 16 days, and clone E's cessation of inflorescence growth extended over 29 days.

The similarity of the three events—leaf cessation, twig cessation, and inflorescence cessation, and their differences from the other six phenological events—was suggested by the ranges and means in

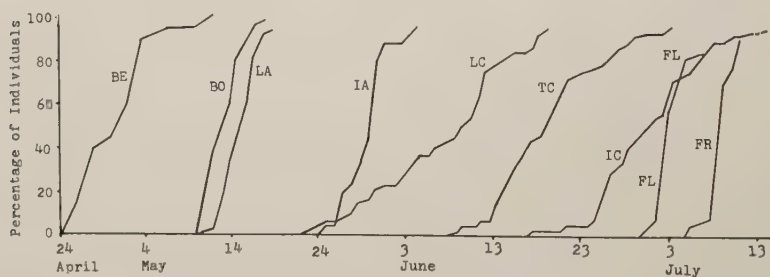


Fig. 1.—Progress of phenological events in clone A. KEY: BE = Bud elongation; BO = Bud opening; LA = Leaf appearance; IA = Inflorescence appearance; LC = Cessation of leaf growth; TC = Cessation of twig growth; FL = First flower; FR = First fruit; IC = Cessation of inflorescence growth.

Table II. The similarity among these events may be more easily seen in Figures 1 and 2 in which the percentage of the sample individuals in one clone which have undergone the specified event are plotted against time. Each series of curves represents the nine events of one

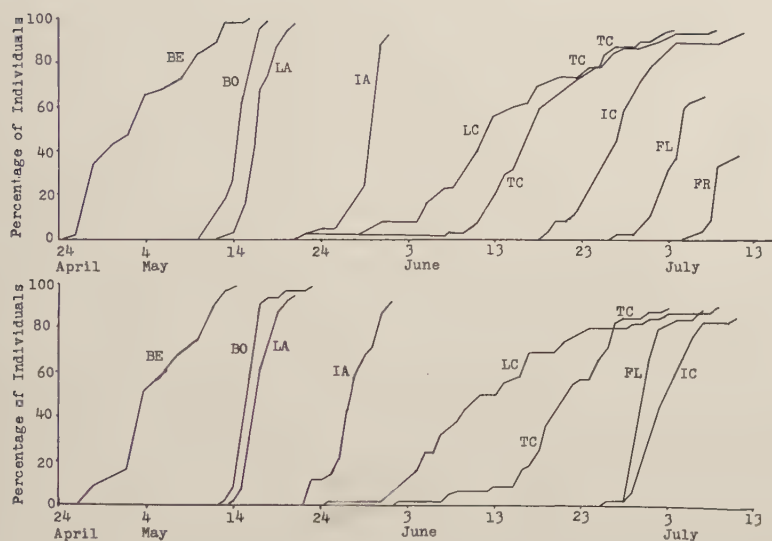


Fig. 2.—Progress of phenological events in clones B, above, and I, below.

clone, and the curves of three clones are shown as examples. The three “cessation” events usually occur over a longer period than the developmental events. The cessations progress more slowly in the clone than do the other events. (The gradually diminishing total represented by the diminishing height of the curves reflects the incomplete development of certain twigs.)

A comparison of the development of one event in one clone with the same event in other clones shows a great similarity between different clones. In most clones, the majority of the buds of the sample twigs elongated within a few days. The most notable exception to this rapidity in development was clone I which showed buds beginning to elongate over a two-week interval. In clones C, D, and F, the duration of bud elongation is lengthened greatly by only a very few individuals. In two clones, G and H, bud elongation was completed before bud opening was initiated. In the remaining clones, bud elongation was essentially complete before the first buds opened. In all clones, the progress of bud opening throughout the clone was similar in its rapidity of development in the clone. Leaf appearance was almost completed in all clones before any of the inflorescences appeared. The appearance of the inflorescence occurred on all stems of a clone within a few days. A few days before or after the appearance of the first inflorescence, a few leaves stopped growing. In some instances (clones A and E) some cessation of leaf growth preceded the appearance of the inflorescence. Cessation of twig growth also began at about this time, in clones D and F, preceding both the first inflorescence appearance and the first leaf cessation. The cessation of twig growth of clone G began before the leaf growth cessation of

that clone. The first inflorescence growth cessation preceded the appearance of the first flower. The progress of inflorescence growth cessation was slow, however, so that both the first flower and the first fruit had appeared in each clone before the last inflorescence had ceased to grow. (In clone F, however, the appearance of the fruit and the cessation of inflorescence growth occurred on the same day.) The first inflorescence growth cessation, first flower, and first fruit usually occurred before twig growth cessation was completed.

Figures 1 and 2 show that there are two types of progress of an event in a clone; rapid, as in bud elongation, bud opening, leaf appearance, first flower, and first fruit, and slow, as in leaf, twig, and inflorescence growth cessation.

ANALYSIS OF PHENOLOGICAL MEANS

The average dates of the different clones for the different phenological events are observed to vary; to determine which variations are significant, Kramer's (1956) modification of a multiple range test was employed. This test permits the grouping of the mean values into those which are and are not significantly different. The means of the clones, represented simply by the clone letter, are arranged in order from early to late. Means which are underlined by the same line are not significantly different, whereas those means not underlined by the same line do differ significantly.

Bud elongation	<u>I</u> <u>B</u> <u>E</u> <u>A</u> <u>C</u> <u>F</u> <u>D</u> <u>G</u> <u>H</u>
Bud opening	<u>I</u> <u>F</u> <u>B</u> <u>G</u> <u>C</u> <u>H</u> <u>D</u> <u>E</u> <u>A</u>
Leaf appearance	<u>F</u> <u>B</u> <u>I</u> <u>G</u> <u>D</u> <u>C</u> <u>E</u> <u>H</u> <u>A</u>
Leaf cessation	<u>B</u> <u>F</u> <u>D</u> <u>G</u> <u>I</u> <u>C</u> <u>E</u> <u>A</u> <u>H</u>
Twig cessation	<u>H</u> <u>I</u> <u>F</u> <u>A</u> <u>C</u> <u>B</u> <u>E</u> <u>G</u> <u>D</u>
Inflorescence appearance	<u>F</u> <u>G</u> <u>E</u> <u>C</u> <u>D</u> <u>A</u> <u>B</u> <u>H</u> <u>I</u>
First flower	<u>A</u> <u>D</u> <u>B</u> <u>G</u> <u>E</u> <u>F</u> <u>H</u> <u>C</u> <u>I</u>
First fruit	<u>D</u> <u>A</u> <u>G</u> <u>E</u> <u>B</u> <u>F</u> <u>C</u>
Inflorescence cessation	<u>G</u> <u>C</u> <u>E</u> <u>H</u> <u>D</u> <u>I</u> <u>A</u> <u>F</u> <u>B</u>

The means which are not statistically different from each other vary from one phenological event to another. An index of the phenological similarity of the clones may be found by investigating the number of times one clone was considered not statistically different from another. Clones C and D and clones C and E show the greatest phenological similarity, since their means are not statistically different in 13 instances. Clone I is least like the other clones phenologically.

The means of the clones for each of the phenological events give a method of designating a clone as "early," "mid," or "late" in comparison with the other clones. If the mean values for all the clones for each event are ranked from early to late, the number of times a clone appears in a certain relative order may be tabulated. (The appearance of the first fruit was not considered, since the two staminate clones did not form fruits.) Clone I, for example, appears among the earliest three clones four times, among the middle three clones twice, and among the latest three clones twice. On the basis of this information, clone I is called an "early" clone. "Early" clones are: B, F, and I; "mid" clones are C and G; and "late" clones are A, D, E, and H.

Data on the age, height, and location of the sample twigs were plotted against different phenological events. The resulting scatter diagrams showed suggestions of both positive and negative correlations, therefore a series of analyses of variance was completed (Table III).

TABLE III.—Analyses of variance

Analysis	Classes between or among which analyses were run					
	All clones	Height classes (0.5 m)	Exposure within clone	Age	Sex	Final twig length
Bud						
Elongation	1%*	NS*	NS	5%*	1%	1%
Bud						
Opening	1%	5%	NS	1%	1%	1%
Leaf						
Appearance	1%	5%	NS	1%	1%	1%
Leaf Growth						
Cessation	1%	NS	NS	1%	NS	NS
Twig Growth						
Cessation	5%	NS	NS	NS	5%	1%
Inflorescence						
Appearance	1%	NS	NS	NS	1%	1%
First						
Flower	1%	NS	NS	NS	1%	NS
First						
Fruit	1%	1%	1%	NS	..	NS
Inflorescence						
Growth	1%	NS	NS	NS	NS	1%
Cessation						

* 1%, significant at 1% level

5%, significant at 5% level

NS, not significant at 5% level

Among all clones, there is significant or highly significant difference for all phenological events. Among the half-meter height classes, there is one event which is statistically highly significant and two events which are significant. Exposure within the clone shows no

statistical significance save in the appearance of the first fruit. Some phenological events are recorded as statistically highly significant and some as statistically not significant when the data are analysed by age groups. Four phenological events are found to be highly significant when information is grouped by sex. Among final twig length classes, six events appear to be highly significant statistically and three not statistically significant.

DISCUSSION

PHENOLOGICAL EVENTS

The earliest event, bud elongation, is one of six which progress rapidly through a clone when once it has begun. Bud elongation, because it is the earliest, is most likely to be affected by changes in the weather during the early portion of the growing season, since it is likely that the weather may be the controlling factor of the environment at that time. Consequently the curve of progress of bud elongation through a clone shows a rapid rate of development interrupted by plateaus which may correspond with periods when the weather was unfavorable for development. The span of time needed for this event to occur, therefore, is greater than the duration of the other five "rapid" events. In analyses of variance, sex and final twig length appeared to show highly significant association with bud elongation. Age appeared to show significant association, and height of stem and exposure within the clone showed no significant association with elongation.

Bud opening is initiated 10 to 16 days following the start of bud elongation in a clone. One of the most rapidly developing events, bud elongation will be observed on all sample stems of a clone often within four days of the first appearance of that event within the clone. Through analyses of variance, age, sex, and final twig length show a highly significant association with bud opening. Significant association is indicated in the case of height, and no significance could be found to be associated with exposure within the clone.

Leaf appearance, like bud opening, is a rapidly progressing event in all clones. There is great similarity from clone to clone in the shape of the curves representing the bud opening and leaf appearance. Only a few days separate leaf appearance from bud opening. Analyses of variance show that age and final twig length have highly significant association with leaf appearance. Significant association appears with height, and no significance is found with sex and exposure within the clone.

Leaf growth cessation is one of the events which progresses slowly through a clone. One may postulate that the causes of initiation of development are of a different nature than the causes of cessation of development and that this is shown by the different nature of the progress of such events in a clone. Though leaf growth cessation usually first appears in a clone following the appearance of the last

leaf of the sample twigs, it is possible, and indeed occurred in clones A and C, for certain leaves to cease growing even before other leaves have appeared. From analyses of variance, one may say that there is a statistically highly significant association with leaf cessation by age, and that no significance may be attached to height, exposure within the clone, sex, or final twig length.

The appearance of the inflorescences in a clone was first noticed at approximately the same time as the first cessation of leaf growth. Leaf growth cessation developed slowly through a clone, whereas the inflorescences appeared within a short time throughout the clone. The rate of progress of inflorescence appearance closely parallels the rate of progress of bud opening and leaf appearance. The sex of the clone and final twig length show statistical evidence of an association with inflorescence appearance. No statistical significance was attached to height, age, or exposure within the clone.

The cessation of growth of the sample twigs in any one clone takes place over a relatively long period of time. The rate of progress within a clone is similar to that of the cessation of leaf growth. In most instances the first cessation of twig growth occurs several days after the first leaves have ceased to grow in that clone, though in clones D, F, and G, the cessation of twig growth appears before the cessation of leaf growth is initiated. In clone D, cessation of twig growth was initiated even before the first inflorescence appeared. Final twig length appears to show highly significant association with twig cessation, the sex of the clone appears to be of significance, whereas the height, age, and exposure within the clone show no statistical significance.

The cessation of growth of the inflorescence is the next event to appear in a clone, though like the cessation of growth of the twig and the leaf, it is an event which develops slowly through the clone. The curve representing the progress of the event shows a rate of development similar to the rate of progress of the cessation of growth of the leaf and the twig. Final twig length appears to have a highly significant association with the cessation of growth of the inflorescence, whereas no significant association can be shown in the cases of the height, age, sex, and exposure within the clone.

Flowering and fruiting both follow the first cessation of growth of the inflorescence and develop rapidly in the clone, once they have begun. The interval between the appearance of the first flower and the appearance of the first fruit is remarkably constant, approximately one week. Analyses of variance show that there appears to be a highly significant association of the sex of the clone with its date of first flowering, but no statistically significant association with height, age, final twig length, and exposure within the clone. No statistical significance is seen with age or final twig length.

The most remarkable feature of *Rhus* phenology is the similarity of events from clone to clone. The relative time of appearance and rate of progress of the event is much the same for all clones.

The phenological events are of two types, initiation events, which develop rapidly within a clone, and cessation events, which develop slowly within a clone.

PHENOLOGY OF THE CLONES

The series of phenological phases of one clone follow each other at intervals which are fairly uniform from clone to clone. Within one clone, one event is usually essentially completed before the next is initiated. The cessation events overlap others more often than do the developmental ones.

When the average values for all clones for each event are grouped together, the clones which fall together cannot be said to be statistically the same, but are said to be not statistically different. Clones C, D, and E which are often grouped together may be said to respond to similar environmental factors in a phenologically similar manner. Clones G and H represent another group which shows some phenological similarity. Clone B does not appear very similar to others in phenology, but may be said to be phenologically intermediate between clones G and H and clones F and A, which tend to respond in a similar manner phenologically. Clone I is least often associated with others in terms of the phenological responses. Apparently phenological similarity is but one manifestation of physiological and genetic similarity and similar phenological responses may be used as another criterion in attempting to determine the taxonomic position of a plant.

Aspects of the structure and life history of a clone show a varying association with its phenology. Though in four events the age of the stem appears to show a significant association, yet other events seem unassociated with age. The height of the stem above ground appears to have significance in three events, and these events share two in common with those significantly associated with age. The sex of the clone appears to have a significant association with six events, but no association with two others. Similarly, the final twig length may bear an association with six events. Exposure within the clone appears to be of significance in only one instance, yet the fact that the appearance of the first fruit is significantly associated with exposure within the clone perhaps is more of a coincidence than an evidence of a direct association.

By studying clones located on and about one hilltop, some variation in the environment was assured. There appears to be no correlation with position on the hill, however, although an analysis of variance shows significant difference among all clones for all phenological events. Among the clones ranked as "early," one finds a southerly exposure, a northerly exposure, and one level clone represented. Similarly among those clones considered "late," one grows on a southerly and one on a northerly slope. This would indicate that whatever the factors of the environment may be which differ from a north to a south exposure, they have no observable effect on the phenology of these sumacs. The significant difference shown

among the clones by the analyses of variance must therefore be caused by genetic differences among the clones.

There can be little comparison drawn between the present study and previous work in plant phenology. This study is an outgrowth of previous attempts to find a correlation between phenology and environmental factors. Previous work has attempted to find phenological correlations with temperature (Brendel, 1859), moisture (Hiley and Cunliffe, 1922), and light (Leibundgut, 1954). The present study has made no attempt to state the precise temperature, light, or moisture regime which the observed clones have undergone.

Clausen and Hiesey (1958) have shown that though the order of bloom of flowers in a transplant garden may vary from the order under natural conditions, yet the order of bloom remains constant from year to year. McMillan and Pagel (1958), working with *Symphoricarpos*, found that those clones which tended to be early or late in their natural habitat frequently retained this characteristic in a common garden. The work of Morris, Silen, and Irgens-Moller (1957) with the bursting of Douglas-fir buds also points out the hereditary nature of the prime control of plant phenology. The present study substantiates the primary importance of heredity in controlling events in the sumacs.

CONCLUSIONS

The phenological variability which exists in local species of sumac, *Rhus glabra*, *Rhus typhina*, and intermediates between the two, is not controlled by any one factor, though the most important control over their phenology is exercised by the genetic constitution of the plant. To a lesser extent, the structure and life history of the plant seem to affect its phenology. The sex of the clone, the height of the stem above ground, the age of the stem, and the final twig length show association with some of the phenological events. The events affected are not the same in each instance, though the opening of the bud was associated with all four characters; sex, height, age, and final twig length. Only the exposure of the clone in relation to the hill and the exposure of the stem within the clone seem to have no effect on the phenology of these sumacs.

Phenological events are of two types, those which are soon completed throughout the clone, the rapidly developing events, and those which are slow in developing. Those events which mark the initiation of development of an organ are of the rapid type, and the events dealing with the cessation of growth of an organ are those which occur over a long period of time.

The phenological responses of clones to their environment offer a means of segregating the clones into those which react similarly to similar situations. The phenological similarity of clones may be considered as an expression of the physiological and genetic similarity of the individuals and hence may be used as a measure of the relationship of individuals.

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Habitat Selection and Activity of the Wood Frog, *Rana sylvatica* Le Conte

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ABSTRACT: On the basis of field and laboratory studies, I found that the habitat selected by *Rana sylvatica* in the non-breeding season is one combining a forest canopy and small ponds. Frogs face the water and sit at the edge of the bank on flat, recently submerged litter. They follow the receding water-line as the ponds dry up and move under the loose leaf-litter of the forest floor when the water is gone.

Within the range of field conditions, more frogs are active at high temperatures and relative humidities than at lower ones. They are sedentary and even during "activity" periods are motionless unless they see a prey item or are disturbed.

The typical escape behavior is to dive in a pond and either become concealed in submerged litter or surface some distance away.

INTRODUCTION

Within the geographic range of a species, neither individuals nor populations are uniformly distributed. They may be absent from some habitats because one or more environmental factors exceed their tolerance limits or because they are eliminated by competition with other species. However, local distribution may also be greatly influenced by behavioral responses to various components of the environment which tend to keep the animals within certain types of situations. These responses are collectively known as habitat selection.

The wood frog, *Rana sylvatica*, occurs from Alaska to Georgia and from Labrador to British Columbia and occupies a diversity of habitats including boreal conifer forests, swamps, and upland forests such as oak-hickory and beech-maple. Low temperatures limit its geographic distribution on the north, high ones limit it on the south and oceans are barriers on the east and west (Martof and Humphries, 1959). However, the factors affecting distribution of wood frogs within their geographic range have previously been poorly understood. This paper reports on a study of habitat selection in this species made in southern Michigan from late March to early June, 1957 and 1958, and September and October, 1958.

Acknowledgment:—I am particularly indebted to Prof. F. H. Test of the University of Michigan for his valuable aid, encouragement, and criticism. Drs. C. F. Walker, W. R. Murchie, and S. H. Spurr, all of the University of Michigan, and Dr. Edward Bellis of Pennsylvania State University read the manuscript and offered helpful advice. The National Science Foundation provided predoctoral fellowships during the tenures of which the project was carried out. The Argus Camera Company and the University of Michigan permitted the use of their properties for the study. My wife, Audry, assisted in the field and in preparation of the manuscript.

DESCRIPTION OF THE STUDY AREA

The study area was a tract of land in Washtenaw Co., Michigan (Webster Township, T.1S., R.5E., S.1) characterized by gently rolling hills separated by marshes, bogs and swamps. Some of the higher areas are abandoned fields and pastures; others maintain oak-hickory stands. Two types of swamp occur; one contains chiefly *Picea mariana* and *Larix laricina*, whereas the other consists of hardwoods. A more detailed description of the area is given by Heatwole and Getz (1960) and Getz (1961).

Most of the investigation was carried out in the hardwood swamp as it was the only habitat supporting a large population of wood frogs. Its dominant plants were *Ulmus americana*, *Acer rubrum*, and *Betula lutea*. The canopy was relatively open and the shrub layer not well developed, although *Rhus vernix*, *Ilex verticillata*, and young dominants were occasionally present. The herbaceous layer consisted chiefly of ferns (*Osmunda regalis*, *Osmunda cinnamomae*, *Onoclea sensibilis*, *Dryopteris spinulosa*), skunk cabbage (*Symplocarpus foetidus*) and mosses. Less common ground-layer plants were *Caltha palustris*, *Coptis groenlandica*, *Trientalis borealis*, *Maianthemum canadense*, *Boehmeria cylindrica*, *Impatiens capensis*, and *Vaccinium angustifolium*. The substrate was Rifle Peat (Veatch *et al.*, 1930), a black, mucky soil consisting chiefly of organic matter. Two soil samples gave pH values of 5.2 and 4.8.

Different parts of the hardwood swamp varied in ground vegetation, topography of the forest floor, and density of canopy. Accordingly, the area was divided into three sections, hereafter designated as the northern, middle and southern sections. The northern section had a more open canopy and denser herb stratum than the southern one. The most conspicuous difference among the three areas, however, was relief of the forest floor. In the northern section there were scattered depressions which were filled with water in the spring and early summer. Mounds surrounded the bases of trees. By contrast, the southern section had a relatively flat floor and contained fewer mounds and depressions. The middle section was intermediate in all respects.

The forest floor of the swamp was classified into several categories on the basis of moisture conditions and litter structure. They were: 1) open water; 2) areas of standing water choked with partly floating leaves; 3) emergent areas which had been previously inundated and on which the leaves were limp, soft and partly decayed, forming a compact, soggy mat with few interstices; and 4) litter which had never been covered with water and which contained many interstices.

An expanded line intercept (50 m long) of the forest floor in each section was used to obtain a quantitative estimate of the relative area occupied by these forest floor types. In April the southern part contained very little open water and most of the area was above water level whereas the northern part contained much open water and many ponds choked with leaves, but relatively few emergent sites (Fig. 1). By late May the amount of water in both places was much reduced.

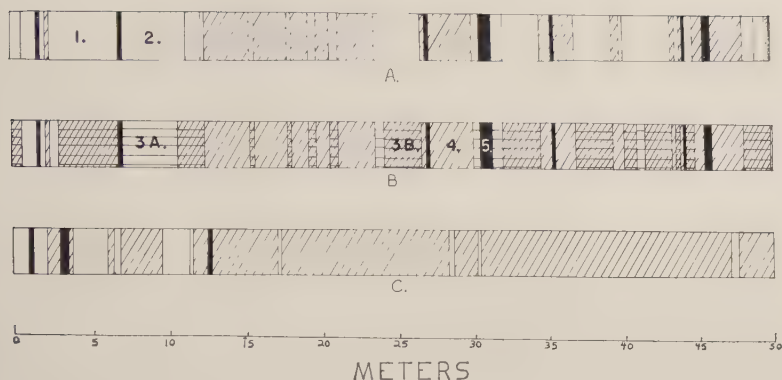


Fig. 1.—Expanded line-intercepts of the forest floor in the hardwood swamp. A. Northern section, April 20, 1958. B. Same line-intercept on May 29, 1958. C. Southern section, April 23, 1958. 1. Standing water. 2. Standing water choked with partly floating leaves. 3a. Previously submerged litter (dry). 3b. Previously submerged litter (wet). 4. Litter which had never been submerged. 5. Moss.

Weather data were recorded by three rain gauges and a Frieze constantly-recording Hygrothermograph in each of the sections except the middle one. In the northern section, the daily temperature maximum in late September was usually between 15° and 20° C; the minimum about 5° C. By mid-October maxima had fallen to approximately 13° - 15° C with minima still about 5° C. In late October temperatures were further lowered to 10° and 3° C for maxima and minima, respectively. The spring daily maxima were usually between 20° and 25° C; minima commonly between 0° and 10° C. The patterns of fluctuation in the northern and southern sections were similar although the latter usually had slightly higher air temperatures.

Relative humidities in October were 80 per cent or above much of the time and dropped as low as 40 per cent only during the afternoon, if at all. Virtually the same pattern was present in the spring except that high humidities were less frequent during the day. Night relative humidities were generally between 80 and 90 per cent in late April and early May. In late May the air was completely saturated at night.

There was no significant difference between the northern and southern sections in amount of rainfall reaching the forest floor.

A more detailed account of weather conditions is given by Heatwole (1959).

NATURE OF THE POPULATION STUDIED

A sample of 61 frogs was captured in the northern part of the swamp during the spring of 1957 to ascertain population structure. The range in body length was 26 to 44 mm, the latter concurring with size of adults in the same region given by Martof and Humphries

(*op. cit.*). There were two size groups, (1) young of the previous season (less than 34 mm s-v) and (2) juveniles more than one year old and adults. In the latter group, frogs of different year-classes could not be distinguished because of overlap in size between individuals of different ages. Fifty-nine per cent of the total population was in the first-year group indicating a heavy mortality before the second year.

LOCAL DISTRIBUTION AND HABITAT SELECTION

Field work was always initiated one week after cessation of breeding so that the local distributional pattern would not be obscured by the aggregation of mature individuals at breeding ponds.

An intensive search was made of all habitat types in the area. No wood frogs were in open areas such as pastures or fields and large populations occurred only in the hardwood swamp. One frog was at the edge of a bog mat, several were around ponds in oak-hickory forest and one was in a conifer swamp. However, in Minnesota, Bellis (1957) found large populations inhabiting a spruce-tamarack bog, and farther north conifer forest is commonly occupied by this species. Two possible explanations are (1) that there is geographic variation in habitat selection or (2) that wood frogs will inhabit conifer habitats only if hardwood swamp is not available. The first hypothesis has merit as Martof and Humphries (*op. cit.*) found morphological differences between Michigan populations and those farther east or west. Differences in habitat preference might parallel such structural differences. However, northern populations which are morphologically similar to Michigan ones inhabit conifer forest. More data are needed to decide between these two hypotheses.

Ecotonal areas between hardwood swamp and open areas received special attention. Only 33 wood frogs were found in the swamp-marsh ecotone; all but one were beneath the shade of trees at the swamp's edge. The single exception was in the open marsh approximately 50 feet from the nearest shade. Two individuals were found in the ecotone between marsh and oak-hickory; both were under trees. Thus it appears that one factor involved in habitat selection by *R. sylvatica* is the presence of arborescent vegetation. This probably has a greater influence than type of substrate or low vegetation as both of the latter were essentially marsh-like in the ecotones.

Abundance of wood frogs in the three sections of the swamp was compared by walking through each section and counting the number of frogs seen. Population density was higher in the northern section, with lesser numbers in the southern one and an intermediate number in the middle section (Table I). Frogs were not completely absent from the southern section as Table I suggests as a few individuals were found there on other occasions. For any given day, data in Table I are comparable between sections because sampling of the three parts occurred within several minutes of each other. Different days should not be compared as sampling was done at different times each day.

TABLE I.—Mean number of frogs observed per minute (amount of time spent in each section was usually about 15 minutes)

Date (1958)	Northern section	Middle section	Southern section
April 30	3.1	—	0
May 4	0.7	—	0
May 9	2.5	0.9	0
May 11	5.4	0	0
May 13	5.7	—	0
May 15	—	0.4	0
May 17	6.3	0.6	0
May 25	2.7	0	0
May 27	1.3	0.1	0
May 31	—	3.0	0

The litter was removed from a 6 m by 10 m plot in the southern section and from two of the same size in oak-hickory forest. Frogs were absent from all of them indicating that the low population densities observed in these areas were real rather than simply resulting from greater difficulty in finding frogs there than in other places. A permanent plot of the same size in the northern section yielded 5-35 frogs per observation period.

The northern section had a greater number of ponds than other wooded places and I believe this to be the factor responsible for its higher population density. Supporting evidence was obtained from studies on the permanent plot mentioned above. Frogs within it were periodically watched through binoculars from a platform built in a tree adjoining the site. Their locations were plotted on a map at the end of each observation period after all had been engaged in their normal activity for at least an hour and no longer gave evidence of being disturbed by my presence. Some frogs were probably overlooked or were hidden as the number counted varied from day to day. With the exception of 6 observations, all frogs were always within 15 cm of the pond's edge on either wet, compact litter or emergent sticks (Fig. 2). As the ponds dried up, they followed the receding water-line and maintained their locations at the water's edge.

The orientation of 79 per cent of frogs captured or observed during the study was toward the water; sixteen per cent faced away from it and 5 per cent were parallel to the shore.

In order to determine the interaction of substrate moisture and litter structure in influencing habitat selection, the following experiment was performed. Two boxes (90 cm x 60 cm x 17 cm) were filled to a depth of 3.5 cm with muck taken from the northern section. In one-half of each box the muck was left bare. In one of the boxes, half of the area was covered with a 3 cm layer of litter from the northern section. The other box had half of the surface covered with small pieces of bark lying loosely on the soil. Both boxes were covered with plate glass except for an opening 5-10 cm wide at each end. These were covered with screen. The boxes were placed in a window-

less room where temperatures ranged from 15° to 20° C and relative humidities from 22 to 54 per cent. Lights were kept on continually. A series of 6 frogs from the northern section was used. A rotation system was employed in which a given frog was kept in the experimental box 48 hours, after which it was replaced by another animal.



Fig. 2.—Position of wood frogs on a 6 m by 10 m plot in the northern section of the hardwood swamp. A. April 22, B. April 27, C. April 29, D. May 4, E. May 6, F. May 10. Elevated areas and sticks outlined with solid lines; compact litter with dotted line. Open water represented by small v shaped marks. Shaded areas represent bases of trees. Arrows represent frogs and point in the direction the animals were facing. Elevated areas contained litter which had never been submerged.

The experimental periods were divided in two parts; an initial period of 23-34 days during which the substrate was kept continually wet. This was followed by a period in which materials in the boxes were no longer watered and drying was allowed to continue for 20 days. The results from the second period were separated into sub-periods of 10 days each for comparison between different levels of substrate moisture. In the box containing leaves, the experiment was repeated for the wet and the first dry period and the results of the duplicate

runs grouped together. In the box with bark the first and second dry periods were repeated. In both instances the results of duplicate runs were similar.

During the wet period (114 observations) frogs were always on the surface of the substrate in both boxes. In the early sub-period of the drying stage (80 observations) frogs were found on the surface in 91 per cent of the observations and under bark or leaves 9 per cent. With further drying of the substrate (34 observations) the percentage of observations in which they were under cover increased to 29 (71% on surface). Thus, reduced substrate moisture influenced microhabitat selection by stimulating the frogs to seek cover where more moist conditions prevailed. When substrate moisture was continually high a decided preference was shown for bare humus rather than leaves. In the wet period, 81.6 per cent of the observations were of frogs on the humus side of the container and 18.4 per cent of frogs on leaves. It appears that *R. sylvatica* responds to the structure of the substrate and inhabits a flat surface unless adverse moisture conditions force it to seek cover.

The litter was removed from an 8 square meter plot on each of three days (Oct. 6, 13, and 18). The ponds had dried up and on October 6 places which had been pond bottoms were now areas of exposed, decayed leaves. Abscission was just beginning. Frogs were absent from the former pond-bottoms and were now under leaf-litter on elevated sites. This situation did not change even after abscission had been completed and all areas were covered with a carpet of leaves (Table II). Apparently by the time newly-fallen leaves were abundant

TABLE II.—Number of frogs per square meter in excavated plots in the northern part of the hardwood swamp

	Oct. 6	Oct. 13	Oct. 18
Elevated area with cover	0.75	0.50	0.13
Dry pond-bottom without cover	0	0	0
Air temperature at noon (°C)	17.5	15.5	6.0

enough to provide shelter in the dry pond-bottoms, temperatures were low and the frogs too sluggish to make any large-scale return. On October 6 (temperature 17.5° C) five of the six frogs hopped from under the litter as I was excavating near them. On October 13 (15.5° C), the frogs were all inactive and did not move even when the leaves were removed from above them. On October 18 (6° C) a single sluggish frog was found beneath the litter on muck. Temperatures given here are noon air temperatures. Hence they were near the maximum for the day and the frogs' activity probably at its daily peak when the plots were excavated.

The decrease in number of frogs in the plots during October may perhaps be associated with movement into the muck for overwintering as Wright (1914) gave October 30 as the latest date that wood frogs were seen in an 8-year study at Ithaca, N.Y. In southern Michigan,

Blanchard (1933) reported *R. sylvatica* under leaves on November 9, associated with other amphibians in what he considered overwintering groups.

ACTIVITY

The activity of poikilotherms is governed to a large extent by body temperature and hence by environmental temperatures. Within the range of field conditions in the spring, more frogs were observed at higher temperatures than at lower ones (Fig. 3). The same was true for relative humidity (Fig. 4). However, the higher temperatures were often accompanied by low humidities and vice versa. Hence each factor tended to modify the effect of the other and a broad scatter of points resulted on Figures 3 and 4.

Two groups of frogs were periodically observed during a 24-hour period (May 17-18, 1958). The first group consisted of those in the swamp and was sampled by counting the number of frogs observed in the range of lantern light (or an equal distance in daylight) on either side of a predetermined path 25 m long. The second group was made up of individuals on an elevated, open area adjacent to the swamp. This site was characterized by an abundance of *Impatiens capensis* 10-15 cm high. During the night a Coleman lantern hung from a tree limb about 1.5 m above the ground at one edge of the clearing and provided faint illumination. At hourly intervals I walked across the clearing and counted the number of frogs seen.

During the night few frogs were seen in the swamp but at sunrise the number increased sharply even though temperature did not

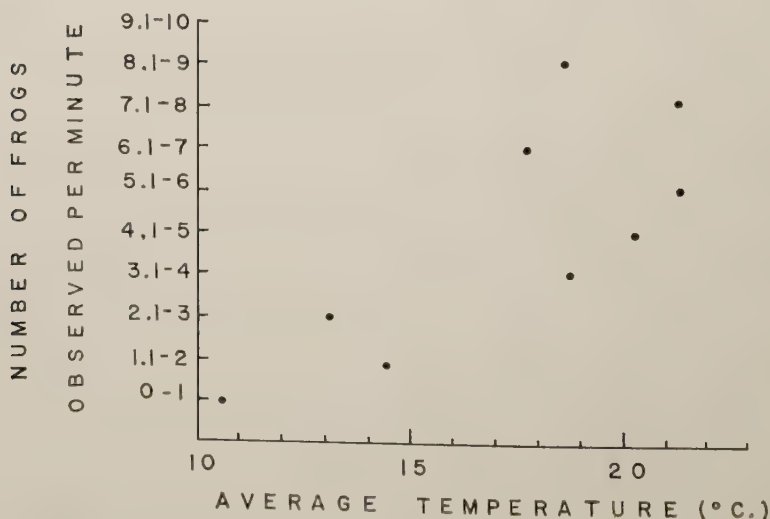


Fig. 3.—Air temperature and activity of wood frogs in the northern section of the hardwood swamp.

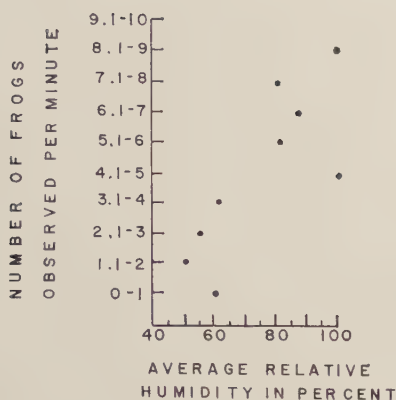


Fig. 4.—Relative humidity and activity of wood frogs in the northern section of hardwood swamp.

increase until two hours later (Fig. 5). Frogs first appeared in the clearing during an overcast period of late afternoon, i.e., when both temperature and relative humidity were high. They were there during the night in fluctuating numbers, perhaps because of the light of the lantern, and remained through the morning which was rainy and overcast. After the sky cleared, the frogs returned to the swamp where there were trees overhead.

Frogs in the permanent plot were watched with binoculars from a platform in a tree to observe habitat utilization under natural conditions. Observation periods varied from 1 hour and 20 minutes to 3 hours and 25 minutes. During these periods 11-46 per cent of the frogs did not change location and even during the longest one, 21 per cent remained in the same spot the entire time. These are probably overestimates of wood frog movements as 9-43 per cent changed location when I disturbed them in entering the area and their return to the original sites constituted the only movement recorded for many of them during the entire period (Table III).

The chief factor stimulating activity of undisturbed frogs was the movement of an invertebrate in front of them although feeding did not always occur at such times. Sometimes the frogs only turned their heads or leaned forward.

Excluding movements of animals returning to their original locations after having been disturbed when I entered the area, distances covered were slight. Three frogs moved approximately 1.5 m during an observation period and 7 moved about 0.5 m. All other activity consisted of feeding, moving an appendage, turning around without changing location, or hopping short distances (25 cm or less). It appears that the "activity period" of wood frogs is characterized by their sitting motionless unless some prey item comes within range or they are disturbed. Occasionally an individual would move in response to movement of another frog.

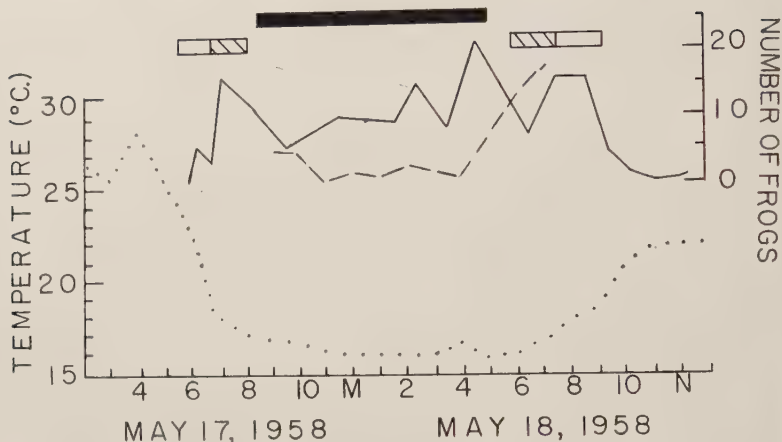


Fig. 5.—Weather conditions and activity of wood frogs on May 17-18, 1958. Solid bar indicates period of darkness; open bar indicates overcast periods and cross-hatched bar indicates rain. Solid line represents number of frogs in clearing at the edge of the swamp. Broken line represents number of frogs along a transect through swamp. Dotted line represents air temperature 3 cm above the ground. M signifies midnight; N signifies noon.

Inactive frogs probably spend their time in submerged litter at the bottom of ponds as several were observed in such situations for long periods. This may account for the variable number found in the permanent plot on different days.

During the springs of 1957 and 1958, the escape pattern of wood frogs was recorded 1,013 times. In 47.8 per cent of the observations the frogs dived into a pond, swam under water for a distance varying from 15 cm to 1.5 m, and then came to the surface where they floated with their heads out of water. The second largest number of escapes (39.4%) followed a similar pattern which ended in the frog hiding in loose, submerged litter in the bottom of the pond instead of surfacing. All other escape behavior involved (1) hopping over emergent litter or muck (11.4%), (2) entering cavities under the bases of trees (0.7%), (3) going beneath logs or sticks on land (0.5%), and (4) diving into ponds and lying on the bottom but not concealed in submerged litter (0.2%).

As most of the frogs faced the water I thought the preponderance of escapes to aquatic situations might simply be the result of their hopping in the direction they happened to be facing when disturbed. To test this hypothesis the escape behavior of 61 frogs was recorded both before and after their capture. When released at their original location but facing parallel to the shore instead of toward the water, the proportion of attempted escapes to non-aquatic situations did not change significantly (Fig. 6). Therefore the direction in which the

frogs faced was not the prime factor determining whether they would enter the water or not. Similarly, handling the frogs did not affect whether they would attempt escape into the water or onto land. However, of those hopping into the water, the percentage of escapes to submerged litter decreased by almost one-half after capture. There was a corresponding increase in the proportion which surfaced. At the time of release the frogs had doubled the exertion put forth during the initial attempt to escape. The consequent increase in oxygen demand may explain the change in behavior.

Escape behavior was not studied in detail after the ponds had dried up. However, casual observation indicated that the most common pattern then was hopping over litter rather than seeking cover beneath it.

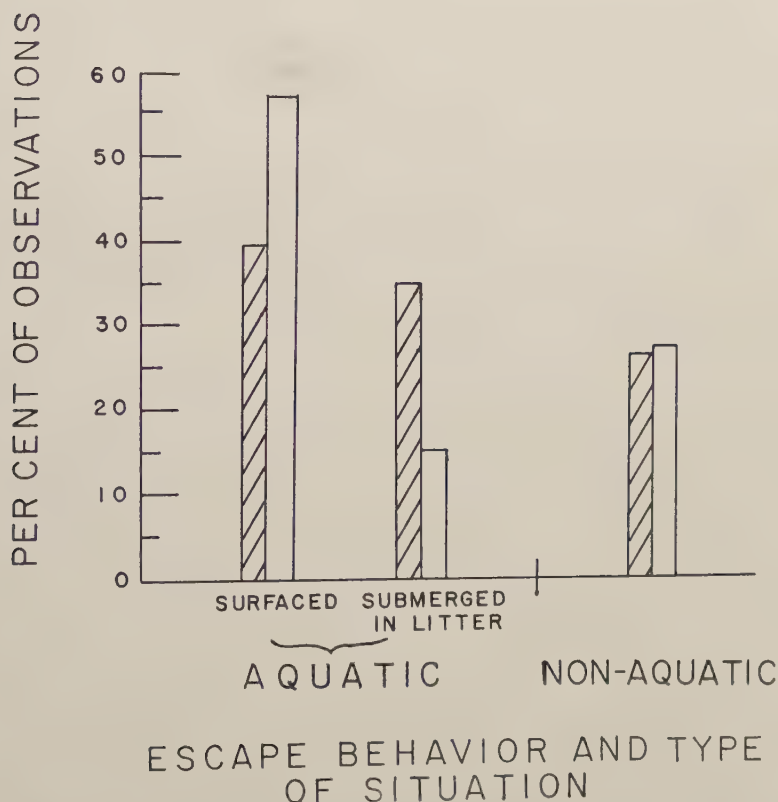


Fig. 6.—Per cent of frogs attempting escape to aquatic and non-aquatic situations. Open bar represents observations of escape behavior before capture; cross-hatched ones escape behavior after capture and release.

TABLE III.—Per cent of frogs displaying activity of various types during observation of the permanent plot in the northern part of the hardwood swamp, 1958 (total for a given period exceeds 100 per cent when some frogs were engaged in several types of activity; numbers of frogs per period ranged from five to thirty-five)

	Apr. 22	Apr. 27	Apr. 29	May 4	May 6	May 10
No change of position or location	21	20	14	11	38	46
Feeding	0	0	0	0	23	3
Alerted but did not feed	16	20	0	0	0	3
Response to movement of other frogs	0	0	0	0	8	0
Reason for change of position or location unknown	42	40	43	67	23	40
Return to original location after disturbance when I entered the plot	21	20	43	22	15	9

DISCUSSION

It is obvious that even in a particular locality no one environmental factor is solely involved in habitat selection. Furthermore, the effect of each specific factor is modified by the action of others and consequently something which is important at one time may become relatively insignificant as seasonal changes in the whole environmental complex take place.

R. sylvatica inhabits forests. Individuals were found in an ecotone between marsh and swamp, but with the exception of one frog, none were found beyond the shade of trees. In the ecotone itself, conditions other than presence of shade were essentially marsh-like. Frogs were active in a clearing on a heavily overcast morning but returned to the adjacent swamp when the sky cleared. The few non-forested habitats from which *R. sylvatica* has been recorded are shaded. For example Black (1938) and Barr (1953) report it from the twilight zone of caves. All of these observations combine to indicate that shade must influence habitat selection of this species. Shady places are characterized by reduced light intensities and temperatures and relatively high humidities. The same is true of overcast periods. Thus, one of these (or a combination of several) are probably directly involved. Not enough data are available to ascertain which one or ones are most important.

Within forested areas, the presence of ponds appears to be the chief environmental feature to which *R. sylvatica* responds. Individuals sit on flat, previously submerged litter at the edges of the ponds and follow the water-line as it gradually retreats during the season. They seem to be reacting to several features associated with ponds. (1) The structure of the newly emerged substrate seems to

be important as under experimental conditions a flat substrate similar to that immediately surrounding the ponds was occupied rather than equally wet leaf-litter. (2) The amount of substrate moisture is involved as caged animals left a flat substrate when it became too dry and sought cover under leaves. (3) The presence of the pond itself governs the orientation of frogs; they tend to face open water rather than the bank.

In the past, frequent observation of wood frogs routed from forest floor litter has led to an exaggerated view of their terrestrial tendencies. The litter is not the preferred habitat but is occupied after drying of more suitable sites around woodland ponds. In some forest types such as oak-hickory, where ponds are frequently small and commonly dry up early in the season, wood frogs might be found in leaf-litter throughout most of the summer.

These remarks do not necessarily apply to this species during the breeding season as other factors are undoubtedly operating then. I have observed breeding aggregations of *R. sylvatica* in ponds as far as one-fourth mile from the nearest forest.

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The Site of *Udonella caligorum* (Trematoda) upon Parasitic Copepod Hosts

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ABSTRACT: The literature indicates that *Udonella caligorum* tends to select the egg strings of the host copepod as a site of attachment in European waters, and the body of the copepod in American waters. Data for two species of parasitic copepods from American waters, having this trematode upon them, confirms the apparent choice of the body of the copepod as a site.

Udonella caligorum Johnston, 1835 is a small leech-like parasitic trematode which apparently spends its entire life upon various species of parasitic copepods of marine fish. It has been reported from European waters (Dawes, 1946); the Atlantic Coast of the U.S. and Canada (Dawes, 1946; Price, 1938; Tortugas (Price, 1938) and Port Aransas, Texas (Causey, 1956) in the Gulf of Mexico; and Monterey Bay, California, (Guberlet, 1936). I add two new records, Ocean Springs, Miss., and Georgetown, British Guiana.

Most of the fish hosts and the parasitic copepods mentioned in the literature are cited (Table I). The fish listed are all marine, and include both cold water and warm water types, ranging widely over the class. Three suborders (following Wilson, 1932) of parasitic copepods are included: the Cyclopoida, Caligoida, and Lernaepodoida. Free swimming caligids are often caught in the tow, and apparently, according to Dawes' record, the trematodes go with them. Price's careful survey and Dawes' tabulation make it evident that probably only one species of trematode is involved. To one interested in host specificity, ecological relations, and distribution, this association of so many kinds of fish and parasitic copepods, and a single species of trematode is surprising, if not improbable!

With sufficient specimens of infested copepods, one can find all stages of the life cycle of the trematode from the stalked egg to the mature worm. Price states, "The life history of this species, so far as represented in the available material, is essentially the same as that given by van Beneden (1858). Van Beneden gives more stages (less clearly) than Price; Dawes copies Price's figures. The one point in the life cycle which is not evident is the transfer from copepod to copepod. Van Beneden thought the change took place during the free swimming stage of the copepod. That this could occur, unless the transfer took place during coitus of the copepods, seems unlikely. All example of coitus I have found thus far, admittedly few, were taken from the fish surface and not from the plankton. One can consider the possibility, on the basis of free swimming copepods carrying the trematodes, that the transfer occurs after the copepods have settled on the fish. I suspect that this occurs slowly, as I have several

TABLE I.—Fish and copepods associated with *Udonella*

Fish	Copepod	Source
<i>Pleuronectus hippoglossus</i>	Caliges	Van Beneden, 1858
<i>Gadus morrhua</i>	Caliges	Van Beneden, 1858
<i>Trigla gurnardus</i>	Calige	Van Beneden, 1858
<i>Neomaenis griseus</i>	" <i>Argulus</i> sp."	Price, 1938
<i>Gadus callarias</i>	<i>Caligus</i> sp.	Price, 1938
<i>Myliobatis californicus</i>	<i>Trebius latituncatus</i>	Price, 1938
Halibut, cod, pollack, wolf-fish, common ling, hake, and flounder	<i>Caligus</i> spp.	Dawes, 1946
Free swimming	<i>C. rapax</i> and <i>C. curtus</i>	Dawes, 1946
Cod	<i>Anchorella uncinata</i>	Dawes, 1946
<i>Carcharias milberti</i>	<i>Alebion carchariae</i>	Dawes, 1946
<i>Amphipholis</i> sp.	<i>Cancerilla vulgaris</i>	Dawes, 1946
<i>Neomaenis griseus</i>	<i>Argulus</i> sp.	Dawes, 1946
<i>Zygaena malleus</i>	<i>Alebion carchariae</i>	Dawes, 1946
Wolf-fish	<i>Caligus minutus</i>	Dawes, 1946
Shadowfish	<i>Anchorella</i> sp.	Dawes, 1946
Ballan wrasse	<i>Caligus labracis</i>	
(Plus other continental hosts).	<i>C. centrodoni</i>	
<i>Pogonias cromis</i>	<i>Caligus haemulonis</i>	Causey, 1956
<i>Galeichthys felis</i>	<i>Lepeophtheirus bonaci</i>	
<i>Pristis pectinatus</i>	<i>Alebion carchariae</i>	

pairs in coitus, with only one of the couple in each case having attached trematodes.

There is a marked difference in opinion between European writers, e.g., Van Benden and Dawes, and American observers, e.g., Price and the present writer, as to where the trematodes are found on the copepods. Van Benden says, "Il habite le corps de plusieurs espèces de caliges, surtout les tubes ovifères des femelles," and his fig. 1 of plate I shows a number of the trematodes attached to an egg string. Dawes states, "Mainly on the egg sacs of female copepod." Price says, "Body and appendages of copepod." It is not customary in technical writing on Crustacea to refer to the egg strings as appendages, and I assume Price means the true, jointed appendages.

Besides a few specimens of *Caligus haemulonis* with trematodes attached to the carapace which came from a drum examined at Port Arkansas, Texas, I have two extensive collections: *Alebion carchariae* Kroyer, 1863 which was taken from *Pristis pectoralis* off Georgetown, British Guiana, by Mr. Harvey B. Bullis, Jr., and *Lepeophtheirus bonaci* Pearse, 1953, which was taken off *Galeichthys felis* at Ocean Springs, Miss., by Mr. J. Y. Christmas. Both collections have a number of the trematodes attached to the copepods, and are the basis of the present paper. The distribution of the trematodes over the bodies of the respective copepods is indicated in Tables II and III.

TABLE II.—Location of *Udonella caligorum* on *Alebion carchariae* from Georgetown, British Guiana

Copepod females with egg strings	2		
Copepod females without egg strings	19	Total number of females	21
Trematodes on carapace	13	Trematode eggs on carapace	0
Trematodes on genital segment	0	Trematode eggs on genital segment	0
Trematodes on egg strings	0	Trematode eggs on egg string	0
		Total number of males	5
Trematodes on carapace	3	Trematode eggs on carapace	0
Trematodes on genital segment	0	Trematode eggs on genital segment	0

There was a total of 44 trematodes on 26 specimens of *Alebion carchariae*. The largest number of trematodes on a particular copepod specimen was 10. As indicated by the Table, all the trematodes were on the carapace, usually attached to either or both borders. (Fig. 1.) No eggs were present. This suggests that it was either too early or too late, probably the former, as most of the trematodes were mature. There were a few very small ones present. The figures indicate that the female is more likely to be parasitized than the male. In addition to the tabulation, the collection included 4 mutilated specimens of copepods, only the carapace being present, with trematodes on 3 of them. No attempt was made to determine the sex of these specimens. There were also 7 loose trematodes in the vial. The latter and the trematodes on the mutilated specimens are not included in the tabulation.

TABLE III.—Location of *Udonella caligorum* on *Lepeophtheirus bonaci* from Ocean Springs, Mississippi

Copepod females with egg strings	20		
Copepod females without egg strings	3	Total number of females	23
Trematodes on carapace	5	Trematode eggs on carapace	3
Trematodes on genital segment	6	Trematode eggs on genital segment	15
Trematodes on egg strings	3	Trematode eggs on egg strings	2
		Total number of males	8
Trematodes on carapace	0	Trematode eggs on carapace	0
Trematodes on genital segment	1	Trematode eggs on genital segment	2

There was a total of 15 trematodes on 31 specimens of *Lepeophtheirus bonaci*. The largest number of trematodes on a particular copepod specimen was 2. Here again the tabulation indicates that the female is the more likely to be parasitized, and with this species

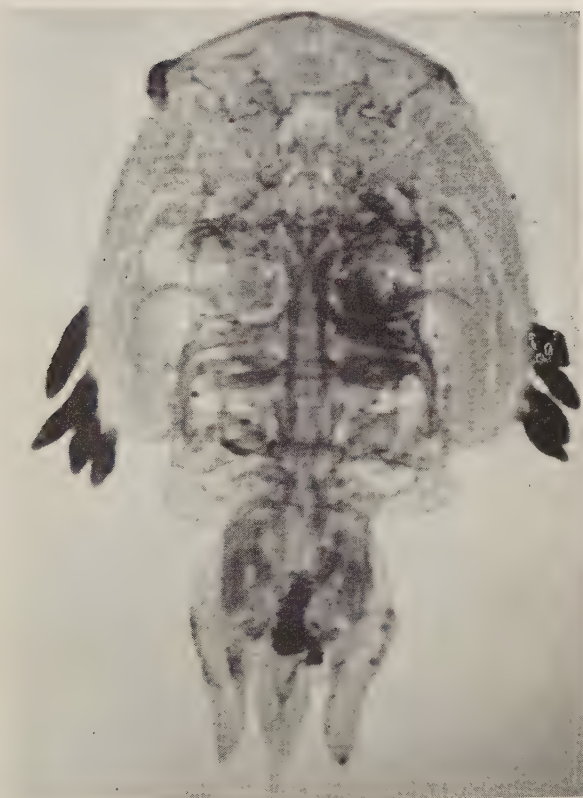


Fig. 1.—*Alebion carchariae* showing 9 specimens of *Udonella caligorum* attached to carapace. Photomicrograph of mounted specimen.

of copepod the genital segment is preferred as a site of attachment. Trematode eggs were present, an occasional egg being attached almost anywhere, but in several examples the eggs attached to the genital segment formed a cluster so large as to almost hide this portion of the copepod body. It will be noted that in this species of copepod trematodes and trematode eggs were found attached to the egg strings. It is evident, however, that in both species of copepod some part of the body is most likely to be selected as a site.

With all due allowance for the uncertainty of what collections received in the mail may actually represent, the literature on this host-parasite relationship indicates a discrepancy. Apparently the stages of *Udonella* occur more often on the egg strings of the host copepod in European waters and on the carapace and genital segment of the host copepod in American waters.

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The Genus *Naematelia*¹

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ABSTRACT: Observations were made on cultures of *Tremella encephala* and on herbarium and field collections of this species. Repeated isolations from the fleshy core and from basidiospores demonstrate that the basidiocarps are composed of two discordant elements. The name *Naematelia*, originally based on this species, is then a *nomen confusum*. The present status of other species is discussed and descriptions and illustrations are given for several species.

In 1816², Fries established the genus *Naematelia* in which he included the single species, *N. encephala* (Pers.) Fries. In this species, the basidiocarps consist of a firm, fleshy core surrounded by a gelatinous hymenial layer, while in other species of *Tremella*, in which genus it had originally been placed, basidiocarps are gelatinous throughout. In his *Systema*, Fries (1822) included two additional species, *N. rubiformis* Fries and *N. nucleata* (Schw.) Fries. Approximately twenty species have been described since that time.

Lloyd (1922) divided the genus into two sections: 1, *Encephala*, including only *N. encephala*, and 2, *Naematelia*, in which he placed *N. nucleata* and *N. globulus* Corda. He discussed thirteen species in addition to the above, but included all under "Other 'Species.'" Lloyd believed that the two sections constituted separate genera, though he did not describe them as such. He also stated that "Tulasne and Brefeld both finding the basidia of *Naematelia* the same as those of *Tremella*, disregarded the heterogeneous structure of the tissue and included the genus in *Tremella*." Others, including Patouillard (1900), Rea (1922), Bourdot and Galzin (1928), Neuhoﬀ (1936), and Martin (1944 and 1952) have followed a similar course, but

¹ I wish to express my appreciation to C. R. Benjamin and J. A. Stevenson, Plant Industry Station, Beltsville; Prof. J. N. Couch, University of North Carolina, Chapel Hill; Prof. R. Heim, Muséum National d'Histoire Naturelle, Paris; Prof. G. W. Martin, State University of Iowa, Iowa City; Stanley Jay Smith, New York State Museum, Albany; and to the Director, Royal Botanic Gardens, Kew; for the loan of specimens used in this study. The research was supported in part by grants from the National Research Council of Canada and the President's Research Committee of the University of British Columbia.

² Fries (1822) cites *Naematelia* Fries as published in Liljebl. Sv. Fl. (1815). This is evidently a reference to the third edition of Liljeblad's *Svensk Flora*, which I have not seen. According to Pritzel, the third edition of this work was published in 1816.

without giving reasons for doing so. Coker (1920), Burt (1921) and Kobayasi (1939) recognized *Naematelia* as a separate genus in their treatments of the Tremellaceae, although only Coker included forms with calcareous "nuclei" such as *N. nucleata*.

A study of *N. encephala* was undertaken in order to clarify its taxonomic position and to learn more concerning its structure. Observations were made on field collections, herbarium specimens and cultures of this and related species. A summary of the taxonomic status of a number of the species is included at the end of this paper.

N. encephala occurs most commonly on coniferous wood such as that of *Pinus*, *Abies*, *Larix* and *Pseudotsuga*. Observations on collections made in British Columbia reveal that this species is usually associated with *Stereum sanguineolentum* (Alb. & Schw. ex Fr.) Fries. In three, of approximately twenty collections made, basidiocarps of the *Naematelia* appeared to arise directly from those of the *Stereum*, rather than from the underlying substrate. Herbarium specimens of this species and of *Tremella tremelloides* (Berk.) Masee (= *Naematelia aurantia*, sensu Burt, 1921) were found to have species of *Stereum* present in many cases. The possibility that the fleshy portion of the *Naematelia* basidiocarps actually belongs to the *Stereum* became apparent. This possibility was strengthened by the fact that a number of species of *Tremella* occur only on the fructifications of other fungi.

Cultures of *N. encephala* were obtained by suspending portions of the hymenia of sporulating basidiocarps over malt agar. Basidiospores landing on the agar germinated by the production of several blastospores (Fig. 1 a). Budding of the latter occurred (Fig. 1 b) and large yeast-like colonies were produced. Transfer of these to other standard media such as malt extract, oat, yeast extract and corn meal agar failed to induce hyphal formation, although the fungus was easily maintained in this yeast-like form and on these media.

Attempts were made to obtain cultures from freshly collected specimens through direct transfer of bits of the basidiocarps. These were removed as aseptically as possible from both the gelatinous and fleshy portions of the fructification and placed directly on media of the types previously mentioned. No cultures were obtained from the gelatinous areas, but the fleshy cores produced rapidly growing cultures in each attempt. Since the hyphae of these cultures did not resemble those of the gelatinous portion of the *Naematelia*, they were compared with cultures obtained through seeding of spores of *Stereum sanguineolentum* on malt agar. The two appeared to be identical. If both the core and the gelatinous portions belonged to a single fungus, one would expect to obtain identical cultures from the two regions and with equal ease.

Malt agar plates were then inoculated with both the yeast-like phase of the *Naematelia* and hyphal cultures of the *Stereum*. Germination of the cells of the former by germ tube (Fig. 1 c) occurred

within a few hours. Haustoria³ (Fig. 1 e) were produced on the hyphae of *N. encephala* soon after dikaryotization and hyphae formed in this manner were identical with those of the hymenial region of that species. At points of contact between the growing hyphae of the *Stereum* and the still yeast-like colonies of the *Naematelia*, compact masses of hyphae were sometimes formed. These appeared woolly externally, but were essentially like the core of the *Naematelia* internally. No basidia were produced, however, nor was a gelatinous layer formed.

It would seem probable that *N. encephala* is parasitic on this, and possibly other species of *Stereum*, though further study of this is necessary. The fact that the core of this species consistently yielded the same fungus, and that this was not the *Naematelia*, demonstrates that the duplex nature of the *N. encephala* fructifications is brought about by the presence of two distinct fungi. The name *Naematelia* is then to be considered a *nomen confusum*, since its characters were derived from two discordant elements. Those species with fleshy cores do not differ in other respects from species of *Tremella*, in which genus they should properly be placed. Those forms with calcareous nodules have been placed in *Exidia*, as noted below.

TAXONOMIC NOTES

All species are listed in alphabetic order. The abbreviations following collection data are those of various herbaria in which the specimens are deposited (J. Lanjouw and F. A. Stafleu, 1956). What is regarded as the correct name is indicated in bold-faced type.

Naematelia atrata Peck

See under *N. nucleata*.

Naematelia aurantia Burt

See under *Naematelia quercina*.

Naematelia cerebriformis Ellis ex Peck

See under *N. encephala*.

Naematelia cinnabarina Mont. Ann. Sci. Bot. III, 10: 120. 1848.

Tremella cinnabarina (Mont.) Pat. Essai Tax. 21. 1900.

Tremella samoensis Lloyd, Myc. Writ. 5: 875. 1919.

Portions of the types of *T. samoensis* and *N. cinnabarina* (both in Lloyd Collection BPI) were examined. There does not seem to

³ These structures were first designated as haustoria by Olive (1946) in discussing a parasitic species of *Tremella*. In a previous paper dealing with that genus (1958) I suggested that, since the structures were to be found in a number of species considered to be saprobic, the use of the term haustorium would be incorrect. However, further study of this group has led me to believe that many of the species previously considered saprobic are actually parasitic on other fungi. The term is accepted here, although some may disagree with its use since the structures are unlike haustoria of fungi parasitizing higher plants.

be sufficient difference between the two to maintain them as separate species.

Naematelia corticola Berk. & Cooke, Linn. Soc. Bot. Jour. 15: 392. 1876.

The type specimen (K) was examined, but no tremellaceous fungus was found. There is a deuteromycete present on the material and the description may have referred to it.

Naematelia encephala (Pers.) Fries, Syst. Myc. 2: 227. 1822.

[*Tremella encephaliformis* Willd. Mag. für Bot. 2(4): 17. 1788].

[*Tremella encephala* Pers. Syn. Fung. 623. 1801 (cites Willd.)].

[*Naematelia encephala* [Pers.] Fries, Obs. Myc. 2: 370, 1818].

Tremella encephala Pers. Myc. Eur. 1: 98. 1822.

Tremella encephaloidea Spreng. Syst. Veg. 4(1): 534. 1827.

Naematelia cerebriformis Ellis ex Peck, N. Y. State Mus. Ann. Rep. 30: 49. 1878.

Tremella alabastrina Bref. Untersuch. 7: 129. 1888.

Naematelia japonica Lloyd, Myc. Writ. 4: L. 54, p. 5. 1915.

Tremella japonica (Lloyd) Yasuda, Bot. Mag. Tokyo 29: 385. 1915.

Naematelia encephaliformis [Willd.] Coker, Jour. Elisha Mitchell Soc. 35: 137. 1920.

Tremella rubiformis (Fries) Quél. sensu Bourdot & Galzin, Hymén. Fr. 25, 1928, fide Neuhoff.

Tremella encephaliformis Willd. ex Olive, Jour. Elisha Mitchell Soc. 62: 66. 1946.

The original and subsequent descriptions of this species were based upon two separate fungi. Therefore, it should be emended as follows:

Parasitic, the basidiocarp in the form of a continuous layer surrounding a fleshy erumpent core formed by the host, gelatinous, the surface minutely roughened to rugose or plicate, sometimes with thick flattened lobes, yellowish, drying pale yellow to cinnamon; hyphae $1.5-4\mu$ in diam., with clamps and haustoria; hymenium amphigenous, the fertile layer extending from the surface to as much as 150μ below it; probasidia borne terminally or laterally, often in opposite pairs along the fertile hyphae, at first subglobose to cylindric or fusiform, mostly globose to subglobose or obovate at maturity, cruciate-septate, $13-20 \times 13-17(-20)\mu$; epibasidia reaching $150 \times 2-4\mu$, swollen to $6-7\mu$ apically; basidiospores broadly oval or subglobose, $(8-)9-11 \times 7.5-9\mu$, germinating by repetition.

Type locality:—Europe.

Habitat:—Commonly adjacent to, or on fructifications of *Stereum* on conifer wood or, less frequently, on angiosperm wood.

Distribution:—Europe, Japan, North America.

Illustrations:—Brefeld, Untersuch. 7, pl. 3, ff. 20-24; Neuhoff, Pilze Mitteleur. 2, Col. pl. 3, ff. 1-12; Bourdot and Galzin, Hymén. Fr. f. 15.

Tremella encephala [Willd.] Bref. var. *steidlerii* Bres., found on oak, was not considered by Lloyd (1922) or Olive (1946) to warrant varietal designation. However, Bourdot and Galzin (1928) elevated Bresadola's variety to specific rank and their illustration

(Fig. 12) suggests that their fungus may be distinct. The type of *N. cerebriformis* (NYS) grew on *Carpinus caroliniana* in association with a species of *Stereum* and does not seem to be distinct from *T. encephala*.

Naematelia encephaliformis [Willd.] Coker

See under *N. encephala*, above.

Naematelia fragiformis [Pers.] Lloyd (as McGinty), Myc. Writ. 7: 1150. 1922.

Tremella fragiformis Pers. Syn. Fung. 2: 622. 1801.

Dacrymyces fragiformis [Pers.] Fries, Syst. Myc. 2: 229. 1822.

Considerable doubt exists concerning this form and Kennedy (1958) lists it under excluded species in her treatment of *Dacrymyces*. Neuhoff (1936) considered it to be the same as *Tremella encephala*.

Naematelia frondosa (Fries) Bonorden, Handb. Myk. 152. 1851.

Tremella frondosa Fries, Syst. Myc. 2: 212. 1822.

Naematelia fuscobasis Lloyd ex Stevenson & Cash, Bull. Lloyd Lib. No. 35, Myc. ser. 8; 32. 1936.

Naematelia fuscobasis Lloyd, *nomen nudum*, Myc. Writ. 7: 1295. 1924.

The type specimen (BPI) does not seem to be a fungus. It consists of what appears to be a resinous exudate externally and is parenchyma-like internally. I could find no indication of fungus hyphae.

Naematelia gemmata (Lév.) Fries, Hym. Eur. 697. 1874.

Tremella gemmata Lév. in Demidoff, Voyage Russie Merid. 2: 95. 1842.

Exidia gemmata (Lév.) Bourd. & Maire, Bull. Soc. Myc. Fr. 36: 69. 1920.

This species has been considered by some (Rea, 1922, Bourdot and Galzin, 1928, and Donk, 1931) to be the same as *Exidia nucleata* Schw.) Burt. However, Neuhoff (1936) felt that it was distinct.

Naematelia globulus Corda, Ic. Fung. 1: 25. 1837.

Tremella globulus (Corda) Bref. Untersuch. 7: 126. 1888

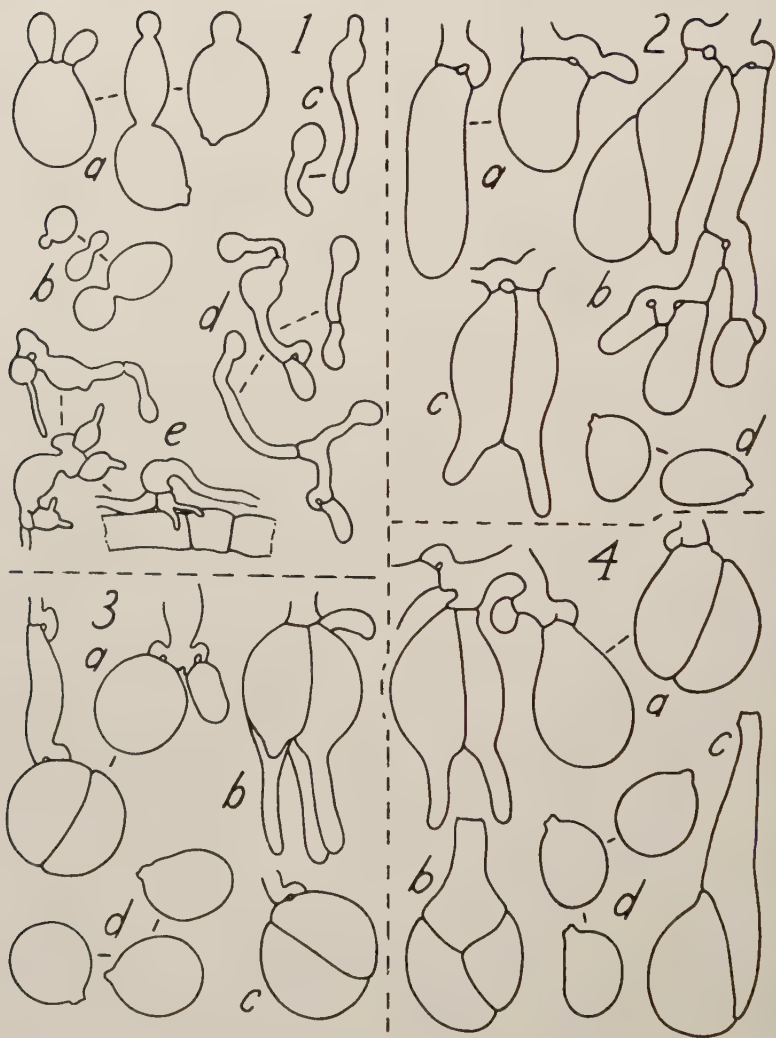
Lloyd (1922) felt that this species is not the same as *Exidia nucleata* [Schw.] Burt, although the description which he gave certainly suggests that it is. As he pointed out, illustrations shown by Brefeld and Corda seem to be of two different species. That Lloyd himself was not certain as to the identity of this species is brought out by his statement (Myc. Writ. 7: 1166) that, "The genus [species], *Naematelia nucleata* (common in the States) and the same (or similar) species, *Naematelia globulus* (very rare in Europe) has never been collected before in a foreign country."

Naematelia guttaeformis Berk. & Br. Linn. Soc. Bot. Jour. 14: 77. 1875.

Tremella guttaeformis (Berk. & Br.) *comb. nov.*

Fig. 2

Fructifications hemispherical, gregarious, minutely roughened, 1-2 mm in diam. or becoming confluent and larger, gelatinous, borne on



Figs. 1-4.—All figures drawn with the aid of a camera lucida and reduced to approximately $\times 1000$. 1. *Tremella encephala*. a, Basidiospores germinating by formation of blastospores. b, Yeast-like budding of cells. c, Germination of yeast-like cells by the formation of germ tubes. d, Fusion of germ tubes of compatible cells. e, Formation of haustoria, one shown attached to a hypha of *Stereum sanguineolentum*. 2. *Tremella guttaeformis*. a-c, Basidia and probasidia in various stages of development. d, Basidiospores. 3. *Tremella tremelloides*. a-c, Basidia and probasidia in various stages of development. d, Basidiospores. 4. *Tremella aurantia*. a-c, Typical basidia and probasidia showing variation in form. d, Basidiospores.

a thin, effused gelatinous layer, 1 cm or more in extent, luteus when soaked, drying horny, castaneous; in section, the hemispherical portions hollow, walls about $300\text{--}400\mu$ thick; hyphae $2\text{--}5\mu$ in diam., with numerous clamps and septa; hymenium forming an amphigenous surface layer; probasidia mostly clavate to subcylindric at first, becoming broadly clavate to elliptical, longitudinally to obliquely cruciate-septate, each with a conspicuous basal clamp through which proliferation occurs; epibasidia about $20\text{--}30 \times 2\text{--}3\mu$; spores ovate, flattened adaxially, $8\text{--}12 \times 5\text{--}7\mu$, germinating by repetition.

Type locality:—Ceylon.

Habitat:—On bark.

Distribution:—Known only from the type locality.

The type specimen (K) seems to be distinct from any described species of *Tremella*. It does not have a fleshy or calcareous core.

Naematelia japonica Lloyd

See under *N. encephala*.

Naematelia nucleata [Schw.] Fries, Syst. Myc. 2: 228. 1822.

[*Tremella nucleata* Schw. Naturf. Ges. Leipzig Schw. 1: 115. 1822].

Naematelia atrata Peck, N. Y. State Mus. Ann. Rep. 24: 83. 1872.

Exidia nucleata (Schw. ex Fries) Burt, Ann. Missouri Bot. Gard. 8: 371. 1921.

Exidia nucleata (Schw. ex Fries) Rea, Br. Bas. 735. 1922.

The type specimen of *N. atrata* (NYS) appears to be a young collection of *E. nucleata*. A specimen designated as the syntype (NYS) is also an *Exidia*, possibly *E. glandulosa* Fr.

Though this species is placed in *Exidia* at the present time, it is no more at home in that genus than in *Tremella*. The structure of its basidia indicates a close relationship with *Stypella*, *Protohydnum*, etc.

Naematelia quercina Coker, Jour. Elisha Mitchell Soc. 35: 135. 1920.

Sparassis tremelloides Berk. Grevillea 2: 6. 1873.

Tremella tremelloides (Berk.) Masee, Jour. Myc. 5: 184. 1889.

Naematelia aurantia sensu Burt, Ann. Missouri Bot. Gard. 8: 368. 1921.

[*Tremella aurantia* Schw. in the sense of various authors, but not of Schweinitz].

Since *T. tremelloides* has long been confused with *Tremella aurantia* Schw., descriptions of both species are given below.

Tremella tremelloides (Berk.) Masee. (Fig. 3)

Basidiocarps hemispherical or elongate, expanded and frequently lobate above, contracted into a narrow base below, the lobes free or united marginally, often flattened and crumpled, plicate, rugose, the surface minutely roughened, yellow to bright orange; in section, outer portion gelatinous, the interior with a whitish fleshy layer of varying width; hyphae of both zones compactly arranged, those of the gelatinous portion $2\text{--}5\mu$ in diam., with abundant clamps and with haustoria; hymenium consisting of a broad but loosely packed zone of basidia borne at the surface or slightly below it; probasidia

at first clavate or obovate, becoming globose to subglobose or obovate at maturity, longitudinally or obliquely cruciate-septate, $14-22 \times 12-18\mu$, borne terminally and the hyphae proliferating laterally; epibasidia $2.5-6.5\mu$ in diam.; basidiospores globose to broadly ovate, $9-12 \times 9-10.5\mu$.

Type locality:—South Carolina.

Habitat:—Associated with species of *Stereum* on wood of angiosperms.

Distribution:—South Carolina, North Carolina, Tennessee, Iowa, Louisiana and Texas.

Illustrations:—Massee, Jour. Myc. 5, pl. 14, f. 1; Lloyd, Myc. Writ. 3, f. 225; Coker, Jour. Mitch. Soc. 35, pl. 23, f. 1 and pl. 58, f. 2; Bresadola, Icones, pl. 1191; Rogers, Univ. Iowa Stud. Nat. Hist. 153, 25, ff. 17-19 and 29, f. 31.

Specimens examined include the type of *Sparassis tremelloides* (K), type of *Naematelia quercina* (NCU) and collections from Iowa, Louisiana, Tennessee and Texas (all IA).

This species does not seem to differ significantly from *Tremella encephala* in its microscopic characteristics. It is possible that the two represent different manifestations of the same species parasitizing two different hosts.

Tremella aurantia Schw. ex Fries, Syst. Myc. 2: 213. 1822. (Fig. 4)

Fructifications typically erect, vesicular-lobate, the lobes crowded, often becoming confluent, hollow, the surface at first minutely roughened, becoming smooth in mature specimens, soft-gelatinous throughout, Orange Buff to Cadmium Orange (Ridgway), fading to pale yellowish on drying; in section, walls of the lobes thick, the hymenium forming an amphigenous layer; hymenium at first covered by a dense layer of conidiophores and conidia, the conidia mostly oval, thin-walled, $3-7 \times 2.5-5\mu$; probasidia at first narrowly clavate, expanding at the apex and becoming capitate or broadly clavate, less commonly ovate or globose, generally with a distinct basal stalk, becoming cruciate or irregularly septate, $(13-15-22(-35) \times 10-15(-17)\mu$, including stalk, forming below the layer of conidiophores and the hymenium thus embedded at first; basidiospores broadly ovate with a large blunt apiculus, $(8-9-10(-11) \times 7-8(-9)\mu$, germinating by repetition.

Type locality:—North Carolina.

Habitat:—Dead wood of angiosperms, associated with species of *Stereum*.

Distribution:—North Carolina, California, British Columbia.

Specimens examined include two collected and identified by Schweinitz, nos. 1107 (Michener Collection, BPI) and 6 (Hooker Collection, K), two specimens from California (IA), and the following from British Columbia; R. J. B. nos. BC-105, -171, -501, -639, -836, -854, -858, -869, and -903.

This species differs from *T. tremelloides* in the size and form of basidia and spores, in lacking a fleshy core and in the possession of a thick layer of conidia in the young basidiocarps. In addition, the

lobes of this species are typically hollow in part, while those of *T. tremelloides* are not.

Naematelia rubiformis Fries, Syst. Myc. 2: 228. 1822.

Tremella rubiformis (Fries) Quél. Fl. Myc. 22. 1888.

Dacrymyces rubiformis (Fr.) Neuhoff, Ark. för Bot. 28A¹: 51. 1936.

Neuhoff considered *N. rubiformis* Fries to be a *Dacrymyces* and listed *Tremella rubiformis* (Fr.) Quél. (in the sense of Bourdot and Galzin) as a synonym of *T. encephala*. Kennedy (1958) lists *D. rubiformis* (Fr.) Neuhoff as a possible synonym of *D. palmatus* (Schw.) Bres.

Naematelia virescens Corda, Ic. Fung. 3: 35. 1839.

Agyrium atrovirens Fries, Syst. Myc. 2: 232. 1822.

Tremella exigua Desm. Ann. Sci. Nat. III, 8: 191. 1847.

Epidochium atrovirens Fries, Summa Veg. Scand. 471. 1849.

Tremella neglecta Tul. Jour. Linn. Soc. Bot. 13: 34. 1871.

Exidia minutula Sacc. Michelia 1: 502. 1879.

Tremella genistae Lib. ex Roum. & Speg. Rev. Myc. 2: 15. 1880.

Tremella atro-virens (Fries) Sacc. Syll. Fung. 6: 790. 1888.

Tremella atro-virens Fries of various authors, but not of Fries, and not *T. atrovirens* Schum. ex Secr. Mycogr. Suisse 3: 282, 1833.

The name *T. atro-virens* (Fr.) Sacc., generally applied to this species, is a later homonym of *T. atrovirens* Schum. ex Secr. The latter was thought by Secretan to be an alga. Corda's name cannot be transferred, since the combination *T. virescens* has been used for another species (see under *N. virescens* Fries, below). *T. exigua* would then seem to be the earliest acceptable name.

Naematelia virescens (Fries) Fries, Hym. Eur. 696. 1874.

Dacrymyces virescens Fries, Syst. Myc. 2: 229. 1822.

Tremella hemisphaerica Secr. Mycogr. Suisse 3: 288. 1833.

Tremella virescens Bref. Untersuch. 7: 128. 1888.

Brefeld considered his species to be the same as *N. virescens* Corda, but from Corda's illustrations it is apparent that the latter was dealing with *T. exigua* (See under *Naematelia virescens* Corda). Fries (1874) transferred *Dacrymyces virescens* to *Naematelia* and listed Corda's species as being the same. Later authors (Rea, 1922, Bourdot and Galzin, 1928, and Neuhoff, 1936) have treated the two as distinct species, however. Fries is sometimes cited as the authority for *T. virescens*, but, since he apparently never recognized such a combination, this is incorrect.

The proper disposition of the following species is uncertain.

Naematelia coccinea Wettst. Verh. Zool.-Bot. Ges. Wien 35: 554. 1885.

Naematelia granulosa Mont. Ann. Sci. Nat. Bot. IV. 1: 144. 1854.

Naematelia morchellaeformis Kalchbr., listed in Sacc., Syll. Fung. 6: 795. 1888.

Naematelia neglecta Tul. in Lloyd, Myc. Writ. 7: 1150. 1922.

I have not found the original description of this and the name could have been merely a herbarium title.

Naematelia nigrescens Mont. in Gay, *Historica fisica y politica de Chile* 8:28. 1852.

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Comments on the Mayfly Genus *Campylocia* with a Description of a New Species (Euthyplociidae: Euthyplociinae)

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ABSTRACT: The status of the mayfly genus *Campylocia* is reviewed and its relationship to *Polyplocia* discussed. Although the two genera are obviously closely related, they can be separated by the use of venational and tarsal differences. *Campylocia dochmia*, a new species from Brazil is described.

Several years ago a small collection of mayflies was sent to the senior author by Dr. M. A. V. D'Andretta, Departamento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil. Included in the lot was a series of specimens, mostly males, of *Campylocia* which represents a new species. To clarify our understanding of the new form, it was necessary for us to make a careful study of available specimens of *C. anceps*, a closely related species. Dr. P. J. Darlington, Museum of Comparative Zoology, Harvard College, and Dr. Willis Gertsch, American Museum of Natural History, have kindly loaned us their specimens of *Campylocia*. Further, Mr. D. E. Kimmins, British Museum (Natural History), furnished us with a sketch of the genitalia of *C. anceps* prepared from the holotype and later used in his study of Ephemeroptera types (1960).³

Campylocia was first described by Needham and Murphy (1924), and the species, *Euthyplocia guntheri* Navás, 1920, *ampla* n. sp., *anceps* Eaton, 1883, and *burmeisteri* Hagen, 1888, were assigned to it. Subsequently, Gros and Lestage (1926) reviewed the family, erecting a new genus, *Longinella*, for *guntheri* Navás, 1920, and although they showed the species *burmeisteri* in their key to the species of *Campylocia*, they did not list it in their table of genera and species of the Euthyplociidae. Ulmer (1932, 1939, and 1942) considered the genus at some length, pointing out that the position of *burmeisteri* was still not clear but that he (1942, p. 104) would consider it to be a synonym of *anceps* ("Ich halte *Burmeisteri* für identisch mit *anceps*."), a conclusion which we accept. He requested Mr. Nathan Banks' permission to examine Hagen's type in the collection of the Museum of Comparative Zoology, but received no reply. We have been privileged to see this specimen of Hagen's, which has attached to it the following note in Hagen's handwriting: "Not named by Eaton. Forceps figure plate IV. f 7d. It is the third single male he saw." Hagen's specimen belongs to the new species we are describing below.

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³ Mr. Kimmins wrote to us with reference to the wings of *C. anceps*, "I have compared the wings of the type with Eaton's figure and consider that he has drawn them accurately."

In 1932 Ulmer concluded that *Longinella* Gros and Lestage = *Campylocia*, thus properly establishing the generic placement of *guntheri* Navás. Further, Ulmer (1942) synonymized *intercalata* Banks, 1918, *guntheri*, and *ampla* Needham and Murphy with *anceps*. No other species have been described in the genus since that date. *C. sikorai* (Vayssière) from Madagascar is retained in the genus by Demoulin (1952).

The most recent review of *Campylocia* is given by Demoulin (1952 and 1953) in which he presents a key to the subfamily *Euthyplociinae*. He differentiates *Campylocia* from *Polyplocia* Lestage, 1921, by claiming that in the mesothoracic wings the bifurcation of MA is clearly beyond that of Rs in *Campylocia* while in *Polyplocia* the bifurcation is practically at the same level. Further, he characterizes both genera as having four-segmented tarsi on the meso- and metathoracic legs. In his discussion of *Campylocia*, he shows that the venation in the wings of *C. anceps* is highly variable in the development of the marginal intercalaries of the radial, anterior median, and posterior median spaces. He cites Ulmer (1939) as doubting the position of the forking of MA and Rs being of any significance in separating the two genera and states that he is in agreement with this conclusion. However, he does believe that the position of the two cubital intercalaries are of much greater value in separating the two genera. In *Polyplocia* the cubitals join CuP, but in *Campylocia* only the longer joins CuA and is generally separated from CuP by at least a sigmoidal vein.

A careful study of our new species clearly indicates that Ulmer is correct in his doubts about the position of the forking of Rs and MA, as in the forewings of our form it occurs at the same level. This character is therefore no longer of use in differentiating *Campylocia* from *Polyplocia*, and if the two genera are really distinct, the only venational characteristic which will serve to separate them is that pointed out by Demoulin and described above.

Ulmer's (1942) detailed analysis of the venation of *C. anceps* clearly shows the degree of variability that is found in the forewing of this species. Our studies of Spieth's specimens reveal that the venational variations are consistent with Ulmer's drawings, especially with reference to the presence of one or two cubital intercalaries. Specimens, apparently taken at the same place and same time, show either one or two of these veins. Where there is a single intercalary it is attached to CuA, while if the second is present it is attached to the first and longer of the two. We have also noted that the forking of Rs and MA is variable as to the distance MA forks distally to Rs. In some of the American Museum specimens, the level of forking is separated by less than the distance of one crossvein from another while at the opposite extreme the forking may be as many as three crossveins apart.

In every available specimen of the species described below as *C. dochmia*, the forks of Rs and MA are virtually at the same level.

Whether this character alone would be of sufficient value to separate this species from *anceps* is questionable.

The metathoracic wing of *Campylocia* has IMP attached to MP₁, CuA, or unattached. Generally MP₂ is attached to CuA and does not fork with MP₁. Again, because of the variability of these veins it may not be correct to use their points of attachment as a generic characteristic. Ulmer's (1939) and Demoulin's (1952) drawings of hindwings of *Polyplocia* show that IMP is attached to MP₂ and MP has normal forking.

While studying the legs of *C. dochmia*, we discovered that the tarsi of the mesothoracic legs are five-segmented rather than four, as claimed by Demoulin for *Campylocia* and *Polyplocia* in his key to the genera. To establish the constancy of this characteristic, we have examined legs from several specimens of *C. anceps* (one of the specimens described as *C. intercalata* by Banks, and several specimens from British Guiana and Surinam which had been studied by Spieth, 1943) and in every case the midtarsus was consistently five-segmented. Whether the discrepancy in the number of tarsal segments on the mesothoracic legs can be used as a further means of distinguishing these two closely related genera must await a study of specimens of *Polyplocia*.⁴

The genitalia of *C. anceps* have been figured by several authors with some apparent differences. The illustration published by Kimmins (1960) should establish with certainty the species with which Eaton was working. Spieth's drawings, made from specimens collected in Venezuela and Surinam, show more details of the genitalic structures. The dome-shaped subanal plate in Spieth's drawing is also variable and the posterior edge of this structure may range from being almost truncate to as curved as illustrated by him. In *C. dochmia* the posterior edge of the subanal plate is broadly truncate and slightly emarginate. The penes of the two species are distinctive, those of *dochmia* having medial lobes that are lacking in *anceps*. A comparison of the genitalia of *dochmia* with Eaton's (1883) figure 7d, Plate IV, leads us to believe that he was dealing with the same forms we are describing below. Although details are lacking in this illustration, the shape of the subanal plate, as he shows it, is very similar to that of *dochmia*.

Table 1 shows that both males and females of *C. dochmia* are generally larger than *C. anceps*. Measurements of *dochmia* were difficult to make because of the way in which the specimens were preserved. The wings were crumpled when the insects were placed in alcohol by packing the whole series in a single vial. Attempts to straighten them for measuring almost always resulted in tearing the

⁴ Dr. Demoulin (personal correspondence, February 15, 1961) has kindly re-examined his specimens of *Polyplocia* and confirmed that the second leg has four movable segments. Segment one is not defined on the dorsal surface of the tarsus and is fused to the tibia on the ventral side. Obviously it is not movable.

membrane. The posterior part of the abdomen of the females is recurved over the back so that their body length cannot be measured with any degree of accuracy.

TABLE I.—A comparison of the size of *Campylocia anceps* and *C. dochmia* (all measurements in millimeters)

	Wing		Body		Caudal filaments	
	Male	Female	Male	Female	Male	Female
<i>C. anceps</i> *	10-14.5	15-32	11-12	22-26	35	
<i>C. anceps</i> **	13-22	34	12-20		55	
<i>C. dochmia</i>	19-22.5	31-35	15-22	22?	52-62	56-64

* Measurements given by Spieth (1943).

** Measurements given by Ulmer (1942). He lists the wing length of only the largest female.

Campylocia dochmia, sp. nov.

MALE

Measurements.—Body-15.0-22.0 mm; forewing-19.0-22.5 mm; hindwing-8.5-9.5 mm; caudal filaments-52-62 mm.

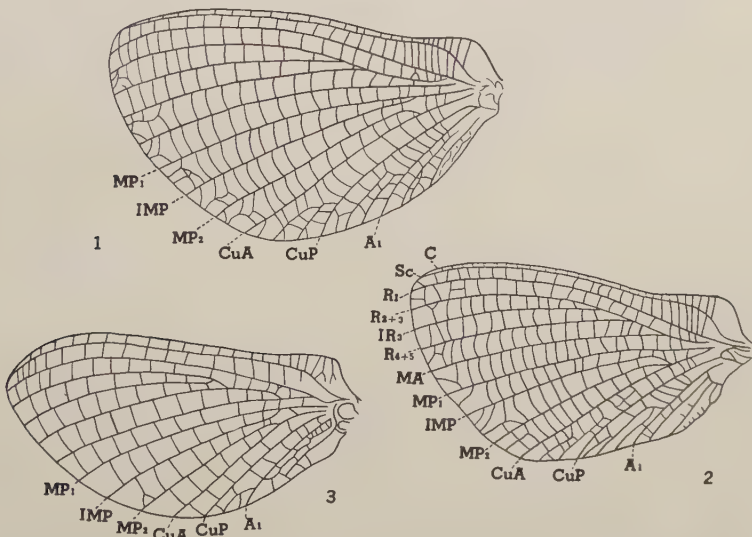
Head.—Purplish brown; vertex between compound eyes heavily shaded with black and with margins and paramedian longitudinal ridges deep purple; occiput light brown with extreme lateral areas and posterior margin suffused with dark purple and with two dark paramedian longitudinal stripes; face and vestigial mouth parts yellowish white, marked with purple. Antennal scape yellow, shaded with purple; pedicel light brown, with several purple longitudinal stripes; flagellum light brown, except whitish near base. Ocelli pale, ringed with deep purple at base. Compound eyes black and placed on stalk-like projections from vertex.

Thorax.—Light brown, with general suffusion of dark purple. Pronotal maculation composed of two areas; anterior one-fourth light brown, suffused with purple, with two small rounded indentations into lateral areas of second, darker area; anterior margin dark; posterior three-fourths of pronotum light purplish brown, with lateral and anterolateral margins dark and with dark transverse stripe on each side paralleling the posterior margin, but some distance from it; from each lateral indentation of first area to this transverse stripe, an oblique lighter area, bounded with purple-brown, which combines with transverse stripe where they meet to form black-brown oblong mark; median area pale, bound with dark brown, which is especially heavy anteriorly, where it is stippled with light brown; immediately lateral to this pale area anteriorly and adjacent to oblique light area, a small light brown triangle, finely bordered with purple; pleura light brown, marked with brown; prosternum yellow-white, suffused with very light purple and with sutures marked with dark purple. Mesonotum light brown, with general purplish suffusion and with

sutures purple; prescutellar and posterior paramedian sutures dark purple; scutellum light brown; triangular area of light brown present on posterolateral areas of scutum; pleura light brown, marked with dark purple, especially around wingbase and coxae; upper anterior region purple, stippled with light brown; mesosternum light brown, suffused with darker brown and with sutures purple; basisternum white, with mediolateral and posterolateral light brown blotches; immediately lateral to the posterior pair, a pair of purple blotches (outside of basisternum). Metanotum light yellow-brown, with median area hyaline and with posterior margin and posterolateral sutures dark purple; pleura and sternum as in mesothorax, except upper anterior region of pleura light brown.

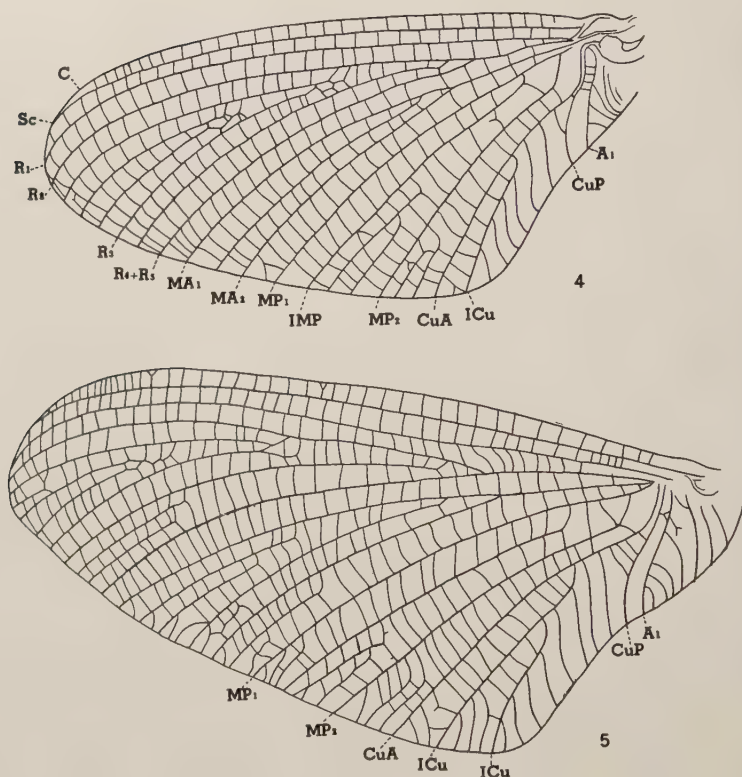
Wings.—Translucent, with purplish tinge, which is especially heavy in costal and subcostal interspaces in forewing. Longitudinal veins light purple; crossveins purplish. Venation as in Figs. 1, 2 and 5.

Legs.—Measurements: foreleg-16.3 mm; femur-4.5 mm; tibia-5.8 mm; tarsus-I-0.4 mm, II-2.1 mm, III-1.3 mm, IV-1.2 mm, V-1.0 mm; midleg-7.7 mm; femur-3.5 mm; tibia-3.1 mm; tarsus-1.1 mm; hind-



Figs. 1-3.—Hindwings of *Campylocia*. 1. *C. dochmia* with IMP attached to MP_1 and MP_2 attached to Cu A. 2. *C. dochmia* with both IMP and MP_2 attached to Cu A. 3. *C. anceps* from Surinam.

leg-8.2 mm; femur-4.3 mm; tibia-3.0 mm; tarsus-0.9 mm. Coloration: foreleg dark purplish brown; femur and tibia with dark longitudinal streaks; tarsal joints whitish and tarsal claws yellow. Mid- and hind-legs similar, except femur shaded with lighter purple. Legs and tarsal claws, as in Figs. 8a, c, e and 8b, d, f.



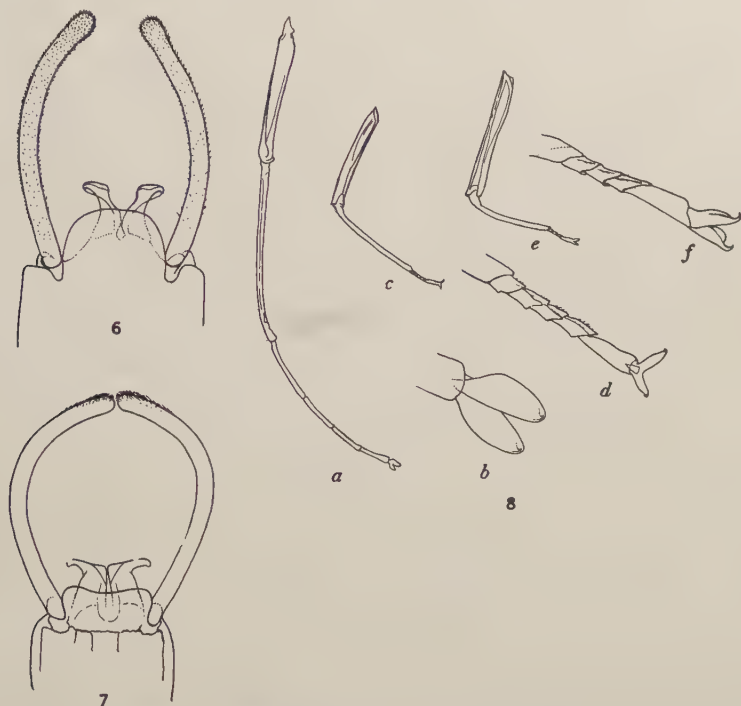
Figs. 4-5.—Forewing of *Campylocia*. 4. *C. anceps* from Surinam.
5. *C. dochmia*.

Abdomen.—Tergites purplish brown, stippled with pale brown and with median stripe, which is hyaline on anterior segments; anterior margin whitish, posterior pale brown; paramedian light, oblique stripe pointing to posterolateral corners, the extreme anterior and posterior ends of which are paler and thus appear as spots; oblique pale stripe arising from anterolateral corners and pointing inward, from the ends of which several very narrow, vine-like lines proceed medially; also, a small pale spot adjacent and slightly lateral to terminal end of this stripe; tergite 9 darker and with markings reduced; tergite 10 slightly paler than 9, with median and lateral stripes of pale brown and with dark brown oblique stripe arising from blackish area adjacent to anterior end of lateral stripes and ending at posterior end of median stripe; posterior margin brownish hyaline. Posterior margin of tenth tergite deeply incised producing broadly rounded median lobe and smaller lateral lobes separated by pale brown grooves. Pleura brownish, with dark brown spiracular markings. Venter pale brown hyaline, generally suffused with brown

laterally, which gradually becomes heavier and more inclusive posteriorly; posterior margin finely bordered with light brown.

Genitalia.—Yellowish white, tinged with purple, as in Fig. 7; forceps shaded with purple.

Caudal filaments.—Purplish, darker basally; joints pale.



Figs. 6-8.—Genitalia and legs of *Campylocia anceps* and *C. dochmia*. 6. Genitalia of *C. anceps* from Venezuela. 7. Genitalia of *C. dochmia*. 8. Legs of *C. dochmia*. a. foreleg, b. tarsal claws of foreleg, c. middle leg, d. tarsus of middle leg, e. hindleg, f. tarsus of hindleg.

FEMALE

Similar to male, with the following exceptions:

Measurements.—Body-22.0 mm?; forewing-31.0-35.0 mm; hindwing-13.8 mm; caudal filaments-56-64 mm. Pronotum with first light colored area extremely reduced; posterior area darker than in male, but with substantially the same pattern. Abdomen with same general maculation as male, but darker.

Holotype, male.—Brazil, Est. Minas Geraes, Sapucaí-mirim (Cidade Azul-1400 mts.), Trav. F°. Nov. 5, 1953. C. Gans and S. Medeiros, collectors. Taken at light and preserved in alcohol. No. 3362.0, University of Florida Collections.

Allotype, female.—Same data as for holotype. No. 3362.0, University of Florida Collections.

Paratypes.—21 males, 1 female. Same data as for holotype. 14 males, 1 female in the University of Florida Collections; 2 males in the collection of Thomas B. Thew; 3 males in collection of Dr. George Edmunds, University of Utah; 2 males in collection of Departamento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil.

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Cyprinid Fishes of the Subgenus *Cyprinella* of *Notropis*. IV The *Notropis galacturus*—*camurus* Complex

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ABSTRACT: The species *Notropis galacturus* and *N. camurus* are redescribed and differentiated from other species of the subgenus *Cyprinella* and synonymies are given. These two species form a distinct unit within the subgenus, distinguished by the presence of depigmented basicaudal areas, a hiatus between nuptial tubercles of the snout and those of the top of the head, two rows of tubercles on each chin ramus, and red pigment in dorsal and anal fins of breeding males. Populations of *N. galacturus* east and west of the Mississippi have differentiated slightly. Lower Mississippi populations of *N. camurus* are racially distinct from those in the Arkansas system. The two species are probably derived from a common stock which became divided into eastern and western portions. *N. galacturus* has crossed the Mississippi, but the range of *N. camurus* appears to have contracted, leaving the two present populations.

The systematic situation in the subgenus *Cyprinella* has been outlined in the first paper of this series, and the two variable species *N. spilopterus* and *N. venustus* treated in subsequent parts (Gibbs, 1957a, b, c). *Notropis galacturus* and *Notropis camurus* stand apart from most of the species of *Cyprinella* as a unit, defined by a number of characters which they have in common. First, and most notable, both have depigmented areas at the caudal base which, at their fullest development, are quite prominent. Occasionally in other species of *Cyprinella* a specimen is found which has such depigmentation, but the character is never common. An unrelated species which is sympatric with *N. galacturus* in the Tennessee system, *Notropis coccogenis*, also has prominent depigmented caudal areas, but this is surely a case of parallelism. The breeding males of both *N. galacturus* and *N. camurus* have greatly enlarged dorsal fins and red pigment in both dorsal and anal. Their tubercle patterns are similar, notably in the lack of a hiatus between the tubercles of the top of the head and those of the snout, in the minuteness of the nape tubercles, and in the presence of two rows on each chin ramus.

This paper redescribes the species *N. galacturus* and *N. camurus*, treats their intraspecific variation, and discusses their possible origin and means of dispersal.

MATERIALS AND METHODS

Specimens used in this study were from the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Cornell University; University of Georgia; Museum of Zoology, University of Michigan; Tulane University; and United States National Museum

(USNM). To staff members of these institutions, I owe my deepest appreciation.

Counts and measurements were made in accordance with Hubbs and Lagler (1958), except postdorsal length (dorsal origin to caudal base) and dorsal origin to lateral line. All measurements were made on specimens between 50 and 60 mm, and are recorded as per cent of standard length.

This paper is based on a doctoral thesis, done at Cornell University under Dr. Edward C. Raney. To him, and to the many colleagues who gave constructive criticism or aid in the field, I extend my sincere thanks.

Notropis galacturus

Whitetail Shiner

- Hypsilepis galacturus*. Cope, 1867:160 (orig. descr.; Holston system, Va.); 1869:229 (Holston system, Va.), 1870:459 (French Broad, Clinch, Cumberland systems).
- Leuciscus kentuckiensis*. Günther, 1868:251 (specimens from Cope from Holston R.).
- Cyprinella galactura*. Jordan and Copeland, 1876:153; Jordan, 1929:81 (char., distr.); Pratt, 1935:76 (char., distr.); Schrenkeisen, 1938:130 (char., distr.).
- Luxilus galacturus*. Jordan, 1877:339, 370, 373 (Tennessee and Cumberland systems); 1878a:294 (char., distr.); 1878b:421, 1879:110 (distr.).
- Photogenis galacturus*. Jordan and Brayton, 1878:18, 64, 91 (Tennessee, Cumberland and Savannah systems).
- Hudsonius galacturus*. Jordan, 1880:292 (char., distr.); 1884:292 (char., distr.).
- Clia galactura*. Jordan and Gilbert, 1883:179 (char., distr., syn.).
- Notropis galacturus*. Jordan, 1885:814; Call, 1887:76 (Shannon Co., Mo.); Jordan and Gilbert, 1887:2 (White R., Ark.); Jordan, 1889:145, 152 (Holston and French Broad systems); Gilbert, 1891:147 (Tennessee system, Ala.); Meek, 1891 (Neosho, White and Black systems, Ark. and Mo.); Kirsch, 1892:291 (Cumberland system, Ky.); Woolman, 1892:266 (Cumberland system, Ky.); 1893:260-267 (Cumberland system, Ky. and Tenn.); Evermann and Kendall, 1895:470 (White system, Mo.); Meek, 1895:77, 82 (White system, Ark.); Jordan and Evermann, 1896b:256 (distr., syn.); 1896a:257 (char., distr., syn.); Smith, 1907:93 (French Broad system, N.C.); Goldsborough and Clark, 1908:35 (Monongahela system, W. Va. — doubtful); Fowler, 1910:283 (variation); Jordan, 1910:58 (char., distr.); Cockerell, 1911:384 (scale illustrated); Evermann and Hildebrand, 1916:444 (E. Tenn.); Jordan, 1916 (char., distr.); Evermann, 1918:364 (Ky. and Tenn.); Fowler, 1923:16 (Catawba doubtful and French Broad systems, N.C., Cumberland system, Tenn.); Pratt, 1923:80 (char., distr.); Pickens, 1928:30 (S.C.); Hildebrand, 1932:66 (Tuckasegee R., N.C.; char.); Kuhne, 1939:50 (Tenn.); Shoup and Peyton, 1940:111, 113 (Cumberland system, Tenn.); Shoup, Peyton and Gentry, 1941:69 (Obey R., Tenn.); Fowler, 1945:115, 343 (N.C., Ala.).
- Erogala galactura*. Jordan, Evermann and Clark, 1930:129 (distr., syn.); Fowler, 1936a:192 (Holston system, N.C.); 1936b:111 (Charter, Tenn.); Driver, 1942:274 (distr., char.); 1950:287 (char., distr.).

Types.—One specimen of *Hypsilepis galacturus*, collected by Prof. E. D. Cope in North Carolina, is located in the U.S. National Museum. This specimen, a male, 83.8 mm, USNM 14981, is herein designated lectotype. In the Academy of Natural Sciences at Philadelphia there are 64 syntypes, ANSP 3381-3444, collected by Cope in the Holston River, Virginia.

Collections examined by river system.—Savannah, 1; Santee, 1; Tennessee, 92; Cumberland, 14; White, 52; St. Francis, 4; Mississippi, 1. Kanawha system collections not seen.

Comparative diagnosis.—*Notropis galacturus* occurs sympatrically with *N. s. spilopterus*, *N. whipplei*, and *N. v. venustus* of the subgenus *Cyprinella*. There are few records of its being taken with *N. camurus*, although in the White system there is apparently a small, perhaps introduced, population of *N. camurus* together with the abundant *N. galacturus*. The differentiation of *N. galacturus* from *N. camurus* may be seen in Tables I-IV. *N. camurus* has fewer lateral-line scales, a smaller predorsal length, accompanied by a longer postdorsal length, a longer head, generally deeper body, as expressed in body depth, dorsal origin-lateral line and caudal peduncle depth, and a slightly larger orbit and longer upper jaw. In addition, the depigmented caudal base of *N. camurus* is much less bipartite than that of *N. galacturus*, often appearing as a bar across the base of the fin rays, and the snout is extremely blunt.

N. whipplei, and particularly *N. spilopterus*, are likely to be the most confusing species. Specimens of *N. galacturus* which have less-prominent depigmented caudal areas very strongly resemble *N. spilopterus*, and in fact, this study has revealed specimens which are surely hybrids between the two.

In the river systems east of the Mississippi, *N. galacturus* differs from *N. s. spilopterus* in the following characters: (1) usually 39-41 lateral-line scales instead of 37-39, (2) usually 15 or 16 pectoral rays, instead of 13-15, (3) a more slender body, usually 21-23% of standard length, instead of 22-26% (4) caudal peduncle depth usually 10-11% of standard length, instead of 11-12%, (5) pigment present along base of anal fin and along the midventral caudal peduncle, (6) the presence from an early age of at least a moderate amount of pigment in all dorsal fin membranes, while *N. spilopterus*, except in breeding males, has little or no pigment in the first three membranes, and (7) the presence of depigmented basicaudal patches.

In the same eastern systems and also west of the Mississippi, *N. galacturus* differs even more trenchantly from *N. whipplei* in most of the same characters. *N. whipplei* has: (1) usually 37 or 38 lateral-line scales, (2) usually 14-16 pectoral rays, (3) body depth 24-28% of standard length, (4) caudal peduncle depth 10-12% of standard length, (5) no pigment along anal base or midventral caudal peduncle, (6) pigment in all dorsal membranes, thus not differing from *N. galacturus*, and (7) no depigmented basicaudal patches.

West of the Mississippi, *N. galacturus* may be distinguished from *N. spilopterus hypsisomatus*, with which it is not sympatric, by its greater number of lateral-line scales, 39 or 40, instead of 35-38; by its 15 or 16 pectoral rays, instead of 13-15; by its smaller body depth, 19-22% of standard length, instead of 10-13%; and by its smaller distance from dorsal origin-lateral line, 12-15% of standard length, instead of 14-19%. In pigmentary differences, the two forms may be told apart as in the comparison of *N. s. spilopterus* and *N. galacturus* above.

Notropis v. venustus, the only remaining *Cyprinella* likely to be confused, has a prominent black caudal spot which *N. galacturus* lacks, and itself lacks the depigmented basicaudal patches of *N. galacturus*.

It might be possible to confuse *N. galacturus* in the Tennessee and Cumberland with *Notropis coccogenis*, which is not a species of *Cyprinella*, but which has a depigmented caudal base. *N. coccogenis* has 2,4-4,2 teeth, and lacks the distinctive *Cyprinella* characters of narrowly outlined scales which appear diamond-shaped, and contrastingly dark posterior dorsal membranes. It further lacks tubercles on top of the head, these being present only at the tip of the snout and lower jaw.

Description.—Teeth 1,4-4,1, hooked, the grinding surfaces narrow, elongate, concave, and usually not serrated. Anal rays 9. Pectoral rays usually 15 or 16. Lateral scales with exposed portions higher than wide. Lateral-line scales usually 39-41; predorsal circumferential scales 13-2-11; caudal peduncle scales 7-2-5. No crowding before dorsal. Dorsal fin moderate in size in non-breeding adults, the first or second principal ray longest, the middle rays longest in the depressed fin; origin nearer caudal base than snout tip.

Head subconical. Orbit usually about 7% of standard length, shorter than snout, 3-4 in head. Mouth terminal or subterminal, oblique, moderate in size; upper jaw reaches about to level of anterior edge of orbit. Upper jaw slightly longer than either lower jaw or orbit. Body, slender, terete, body depth usually 20-23% of standard length. Caudal-peduncle depth usually 10-11% of standard length. Lateral line slightly decurved from opercular margin to below middle of dorsal fin.

Breeding males with scattered tubercles on top of head, snout, and area between eye and snout, most dense in the latter two areas. No hiatus present between head and snout tubercles. Chin rami with two or more rows smaller than those of top of head. Nape tubercles very small; those of rest of notal ridge absent or almost invisible. Extremely small prickles on all body scales except belly, partially arranged in rows on exposed scale margins. Small tubercles on all fin rays, following their branching, often weak in dorsal and caudal.

Coloration.—Dorsal scales and a row or two below the lateral line narrowly edged in black, appearing diamond-shaped. A poorly developed lateral stripe present behind the level of the dorsal fin, the

narrow dark line which marks its dorsal outline continued forward almost to opercle. A very diffuse band, slightly denser than the background color, runs in a straight line from opercle to caudal base, its lower half merging with the lateral stripe posteriorly. A narrow middorsal line present along entire dorsum both before and behind dorsal fin.

The most prominent character of the species is the depigmented caudal base, which takes the form of two patches whose margins extend from the bases of the most-anterior procurent rays to the middle of the junction between scales of caudal peduncle and caudal rays, and out to the distal end of the longest procurent ray (see Fig. 1).



Fig. 1.—Left lateral views of: (top) *Notropis galacturus*, CU 25992, male, 60.3 mm, Tennessee drainage, Franklin Co., Tenn.; (middle) *N. camurus*, CU 23357, male, 61.1 mm, Arkansas drainage, Cherokee Co., Okla.; (bottom) *N. carvurus*, CU 24931, female, 64.7 mm, Mississippi drainage, De Soto Co., Miss. Photography by Douglass M. Payne of Cornell University.

Belly immaculate. Sides of anal fin and midventral caudal peduncle with more or less prominent pigment.

Top of head dark, covered with small melanophores which reach the lower edge of the lachrymal and circle the eye. The upper part of the preopercle and the entire opercle are covered with diffuse, larger melanophores. The pigment of the lips is similar to that of the snout. Remainder of head immaculate. Deep-lying bar of pigment between chin rami hardly visible.

Dorsal fin usually well pigmented on all membranes, the last two noticeably darker than the rest. Caudal lightly pigmented except in basal patches, the pigment along outer edges of rays often very dark, adding to the contrast of the depigmented areas. Pectoral fin rays usually with melanophores lining the leading rays. Pelvics and anal lack pigment.

Breeding males assume a dusky gray cast, all fins are filled with milky pigment, and the anal and enlarged dorsal fin are red.

Intraspecific variation.—Exchange of genetic material between stocks of *N. galacturus* in the Tennessee-Cumberland and those in the Ozark region appears to have been sufficient and/or recent enough to minimize the differences between these portions of the range. Fishes from the two regions, however, show slight but definite signs of drift from one another. These trends are illustrated in Tables I, III, IV. The number of lateral-line scales is different, the mean being 39.50 or less in the Ozarks, 40.00 or more in the East. A slight trend is present in pectoral rays, of which the Ozark populations have slightly more than the East. Among proportional characters, predorsal length, head length, caudal peduncle depth, body depth, and dorsal origin-lateral line show a shift. None of these differences is of such magnitude as to warrant nomenclatorial recognition, or even racial status, although the latter, merely on the basis of geographical isolation would not seem unreasonable.

Range.—Tennessee, Cumberland, and upper Savannah, Santee, and Kanawha systems east of the Mississippi; Ozark Plateau and Ouachita Mountain portions of the White and St. Francis systems west of the Mississippi. One collection in the U.S. National Museum, according to the accompanying data, was made in Wyatt, Missouri. Wyatt is in Mississippi County and is well outside the range of either eastern or western segment of the species. Further, *N. galacturus* habitat is probably not found in this region. Although the record is possible, it must be the subject of considerable doubt.

Habitat.—Cool, clear streams, most commonly in the vicinity of mountains. Although it is most often found in moderate-sized waters, it has been taken on occasion in small headwater streams.

Etymology.—The name *galacturus* is derived from the Greek *gala* (genitive *galactos*), milk and *oura*, tail, with reference to the white basicaudal marks.

TABLE I.—Frequency distribution of meristic characters of *Notropis galacturus* and *N. camurus*

River System	Lateral-line scales										$\bar{x}$	N	SD	SE
	35	36	37	38	39	40	41	42	43					
<i>N. galacturus</i>														
Cumberland	...	...	...	...	13	33	13	1	...	40.0	60	.71	.09	
Tennessee	...	...	...	2	36	116	76	16	4	40.3	250	.88	.06	
Savannah	...	...	...	...	...	...	1	...	...	41.0	1	...	...	
White	...	...	...	5	34	32	3	1	...	39.5	75	.75	.09	
St. Francis	...	...	...	...	4	1	1	...	...	39.5	6	.84	.34	
(Mississippi)	...	...	...	...	1	3	...	...	...	39.3	8	.71	.25	
Total eastern	...	...	...	2	49	149	89	18	4	40.3	311	.86	.05	
Total western	...	...	...	5	38	33	4	1	...	39.5	81	.75	.08	
<i>N. camurus</i>														
Osage	...	4	1	...	...	...	...	...	...	36.2	5	.45	.20	
Arkansas	3	91	60	5	...	...	...	...	...	36.3	169	.76	.04	
Total Arkansas Race	13	95	61	5	...	...	...	...	...	36.3	174	.66	.05	
Lower Miss. Race	...	10	45	29	2	...	...	...	...	37.3	86	.69	.05	
Pectoral rays														
<i>N. galacturus</i>	13	14	15	16	17	18	N	$\bar{x}$	SD	SE				
Cumberland	...	12	58	43	6	...	119	15.4	.73	.07				
Tennessee	...	59	271	167	16	1	514	15.3	.71	.03				
Savannah	...	...	...	2	...	...	2	16.0	...	...				
White	...	9	72	79	10	...	170	15.5	.69	.05				
St. Francis	...	...	6	5	1	...	12	15.6	.67	.19				
(Mississippi)	...	...	9	6	...	...	15	15.4	.51	.13				
Total eastern	...	71	329	212	22	1	635	15.3	.72	.03				
Total western	...	9	78	84	11	...	182	15.5	.69	.05				
<i>N. camurus</i>														
Osage	...	...	6	4	...	...	10	15.4	.52	.16				
Arkansas	4	19	145	150	26	...	344	15.5	.76	.04				
Total Arkansas race	4	19	151	154	26	...	354	15.5	.76	.04				
Lower Miss. race	...	11	81	77	9	...	178	15.5	.69	.05				

Notropis camurus (Jordan and Meek)

Bluntface Shiner

Cliola camura. Jordan and Meek, 1885:474 (orig. descr.; Fort Lyon, Colo.).
Notropis camurus. Cragin, 1885:108 (Neosho system, Kans.); Jordan, 1885:814; 1891:18 (Arkansas R., Wichita, Kans.); Gilbert, 1886:208 (Neosho R., Oswego, Kans.); Jordan and Evermann, 1896b:256 (distr., syn.); 1896a:279 (char., distr., syn.); Gilbert, 1889:39 (Neosho system, Kans.); Jordan, 1899:58 (char., distr.); 1910:58 (char., distr.); 1916:58 (char., distr.); Pratt, 1923:80 (char., distr.); Jordan, 1928:370 (distr.); Moore and Paden, 1950:85 (Illinois R., Okla.); Moore, 1952 (Okla.).
Cyprinella whipplei. Graham, 1885:73 (misidentification).
Erogala camura, Jordan, Evermann and Clark, 1930:129 (distr., syn.).

TABLE II.—Frequency distribution of meristic characters of
Notropis galacturus and *N. camurus*

	Pred. circumf. scales above LL					
River System	11	12	13	14	15	N
<i>N. galacturus</i>						
Cumberland	----	----	55	2	3	60
Tennessee	8	9	215	11	12	255
Savannah	----	----	1	----	----	1
White	----	----	58	6	12	76
St. Francis	----	----	6	----	----	6
(Mississippi)	----	----	5	1	2	8
Total eastern	8	9	271	13	15	311
Total western	----	----	64	6	12	82
<i>N. camurus</i>						
Osage	----	----	1	1	3	5
Arkansas	----	1	85	41	43	170
Total Arkansas Race	----	1	86	42	46	175
Lower Miss. Race	3	4	76	3	1	87

	Anal rays			
River System	8	9	10	N
<i>N. galacturus</i>				
Cumberland	----	56	3	59
Tennessee	18	228	11	257
Savannah	----	1	----	1
White	6	78	2	86
St. Francis	----	6	----	6
(Mississippi)	----	8	----	8
Total eastern	18	295	14	317
Total western	6	84	2	92
<i>N. camurus</i>				
Osage	----	5	----	5
Arkansas	9	157	5	171
Total Arkansas Race	9	162	5	176
Lower Miss. Race	----	81	8	89

Cyprinella camura. Pratt, 1935:76 (char., distr.); Schrenkeisen, 1938:130 (char., distr.).

Notropis camura. Cross, 1954:309 (Neosho system, Kans.).

Types.—*Cliola camura* Jordan and Meek USNM 15256. Fort Lyon, Colo., Dr. E. Palmer. Two specimens were in this type series. One of these, a very highly developed male, 80.0 mm in standard length, with an extremely arched dorsal profile, is herein designated lectotype and retains the original catalogue number. The other is a specimen which had previously been reidentified as *Hybognathus nuchalis placita*. This has been recatalogued as USNM 163962.

Collections examined by river system.—Arkansas, 61; White, 1; Osage, 1; Lower Mississippi tribs. in Miss. and La., 25.

Diagnosis.—Although *Notropis camurus* is sympatric with only two species of *Cyprinella*, *Notropis spilopterus hypsisomatus* and *Notropis v. venustus*, it actually most closely resembles *N. whipplei*.

One would be hard-put to distinguish *N. camurus* from *N. whipplei* on the basis of meristic characters, and proportional characters show few distinctions. The head length is usually 26-28% of standard length in *N. camurus*, instead of 25-26%, and the upper jaw is usually 8-9% of standard length, instead of 8%. Thus it is clear that identification must rest on conformation and coloration. *N. camurus* has the depigmented caudal base, which *N. whipplei* lacks, and has a much blunter snout, although the Lower Mississippi form of *N. camurus* is less extreme in the latter character. Breeding males of *N. camurus* may be distinguished by their red dorsal and caudal fins, and by the lack of a hiatus between tubercles of head and snout (Fig. 2).

From *Notropis spilopterus hypsisomatus*, *N. camurus* may be identified by its 15 or 16 pectoral rays, instead of 13-15; by its larger upper jaw, usually 8-9% of standard length, instead of 7-8%; by its longer postdorsal length, usually 51-54% of standard length, instead of 48-51% (dorsal fin about equidistant between snout and caudal base); and importantly, by its nine anal rays, rather than eight. The blunt snout, depigmented caudal base, and tubercle characters by which *N. camurus* was distinguished from *N. whipplei* will also serve for *N. spilopterus*, and in addition, breeding male *N. spilopterus* have moderately large tubercles on the nape and notal ridge, and lack an enlarged dorsal fin.

N. v. venustus may be easily distinguished by the presence of its black caudal spot and eight anal rays, and by its lack of the contrasting black pigment of the posterior dorsal membranes or depigmented caudal base.

Description.—Teeth 1,4-4,1, hooked, the cutting surfaces narrow, concave, and with or without serrations. Anal rays 9, pectoral rays usually 15 or 16. Dorsal fin moderate in size in non-breeding adults, the third principal ray longest, the rays about equal in the depressed fin; origin about equidistant from tip of snout and caudal base.

Exposed portions of lateral scales higher than wide. Lateral-line scales usually 36-38; predorsal circumferential scales 13-2-11, sometimes 15-2-11. It is worthy of note that a small number of collections show a departure from the count of 11 below the lateral line, which is so dominant in most of the species of *Cyprinella*. These collections have a majority of 12 and 13 counts. Caudal peduncle scales 7-2-5. Scales not crowded before dorsal.

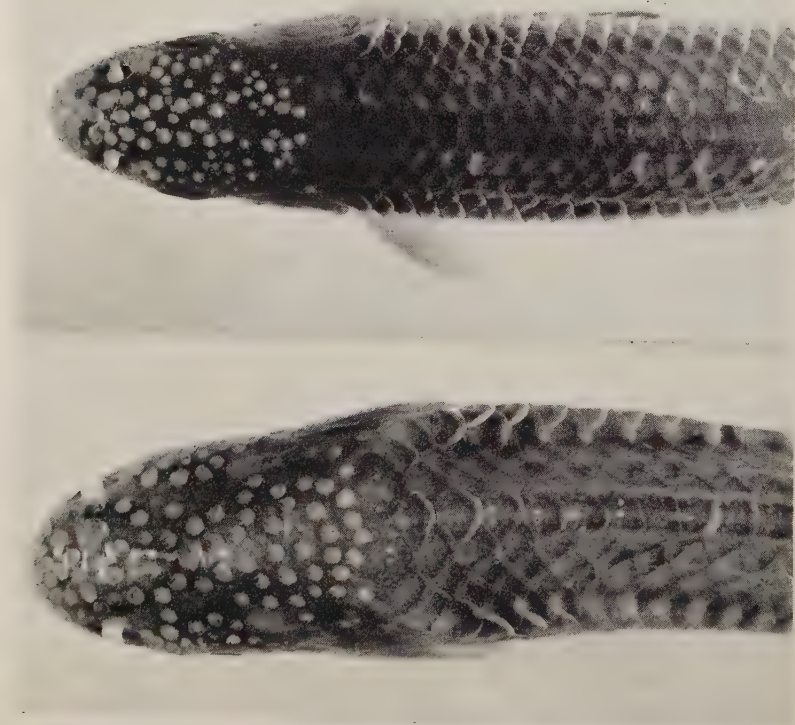


Fig. 2.—Typical breeding tubercle pattern on top of head and back in: (top) *Notropis galacturus* and (bottom) *N. camurus*. The absence of a hiatus between tubercles of snout and those of the top of the head is characteristic of these two species alone among the *Cyprinella*.

Head bluntly triangular. Orbit usually 7-8% of standard length, as long as snout or slightly shorter, $3\frac{1}{2}$ -4 in head. Snout quite blunt and rounded. Mouth terminal or subterminal, oblique, moderate in size, upper jaw usually 8-9% of standard length; the upper jaw usually reaches just behind the anterior margin of the orbit and is slightly longer than orbit.

Body moderately deep, usually 24-27% of standard length, somewhat compressed; caudal peduncle depth 11-13% of standard length. Lateral line slightly to moderately decurved from opercular margin to below posterior part of dorsal fin.

Breeding males with tubercles similar to *N. galacturus*. Head, snout and area between eye and snout with concentrations of scattered tubercles; no hiatus between those of head and snout. Two rows on each chin ramus. Nape tubercles very small, becoming almost invisible on the notal ridge before the dorsal fin. Tiny pearl organs over most body scales and on fin rays, following the branchings.

Coloration.—Lateral scales narrowly outlined in black, appearing diamond-shaped. An indistinct lateral stripe present on the posterior half of the body. A poorly-developed dark humeral bar present, extending from opposite upper opercular margin to base of pectoral fin. Dorsum with a narrow stripe before and after the dorsal fin, extending to the procurent caudal rays. Venter immaculate below a scale row or two under the lateral line.

The depigmentation of the caudal base is not as well defined as it usually is in *N. galacturus*. Commonly it forms a light bar at the base of the caudal rays, flaring slightly dorsally and ventrally. Often it is a shallowly emarginate area, reminiscent of the basicaudal patches of *N. galacturus*.

The dorsal fin is well-pigmented on all its membranes from an early stage, the last two membranes prominently darker than the rest. The caudal fin is lightly pigmented except for the blanché base, and there is sometimes a row of pigment along some of the leading pectoral rays. The pelvics and anal are without melanophores.

Breeding males have red dorsal and caudal fins, and all fins are suffused with milky pigment.

Races.—Two distinct populations of *Notropis camurus* are known, one in tributaries of the Arkansas River, the other in Mississippi River tributaries in Mississippi. Tables I, II, IV indicate that a fairly wide divergence has taken place between these two populations. For example, a line drawn between 36 and 37 lateral-line scales results in an index of divergence of 76.3. A far greater proportion of Arkansas specimens have more than 13 predorsal circumferential scales above the lateral line than do Lower Mississippi fish. In proportional characters, the Lower Mississippi population tends toward a more streamlined form, approaching *N. whipplei*, rather than the straight contours of Arkansas River *N. camurus*. While body depth shows little difference, the caudal peduncle of the Lower Mississippi population tends to be less deep. Dorsal origin-lateral line is somewhat less in the Lower Mississippi forms than in those from the Arkansas, and both eye and upper jaw tend to average larger. By some standards, these two populations might be called subspecies,

TABLE III.—Frequency distribution of body proportions, expressed as per cent of standard length, of *Notropis galacturus* and *N. camurus*

River System	Predorsal length								N
	50	51	52	53	54	55	56	57	
<i>N. galacturus</i>									
White			8	4	3		1		16
Tennessee-Cumberland	1	1	1	8	11	12	1	1	36
<i>N. camurus</i>									
Osage					1	1			2
Arkansas	2	6	14	4	1				27
Lower Mississippi		2	6	6	4	1			19

River System	Postdorsal length								N
	46	47	48	49	50	51	52	53	
<i>N. galacturus</i>									
White		1	4	5	6				16
Tennessee-Cumberland	2	3	12	13	4	2			36
<i>N. camurus</i>									
Osage						2			2
Arkansas				1	3	9	9	4	27
Lower Mississippi				2	5	7	3	2	19

TABLE III.—(continued)

River System	Head length						N
	23	24	25	26	27	28	
<i>N. galacturus</i>							
White	1	6	5	4			16
Tennessee-Cumberland		4	14	15	3		36
<i>N. camurus</i>							
Osage				1	1		2
Arkansas			2	12	11	2	27
Lower Mississippi			2	7	6	4	19

River System	Caudal peduncle depth					N
	9	10	11	12	13	
<i>N. galacturus</i>						
White		2	13	1		16
Tennessee-Cumberland		1	18	17		36
<i>N. camurus</i>						
Osage					2	2
Arkansas				18	9	27
Lower Mississippi			8	11		19

TABLE IV.—Frequency distribution of body proportions, expressed as per cent of standard length, of *Notropis galacturus* and *N. camurus*

River System	Body depth										Orbit length								
	19	20	21	22	23	24	25	26	27	28	29	30	N	6	7	8	9	N	
<i>N. galacturus</i>																			
White	2	4	8	2									16	2	11	3		16	
Tennessee-Cumberland		1	10	12	10	2	1						36	2	26	8		36	
<i>N. camurus</i>																			
Osage												2	2		1	1		2	
Arkansas						3	7	10	6	1			27		17	10		27	
Lower Mississippi				1		4	3	6	4	1			19			15	4	19	

at least on the basis of the divergence in lateral-line scales. The mode of the Lower Mississippi population, however, overlaps the Arkansas population at a high point in the latter's distribution, so that actual separation would be quite difficult. In this study, therefore, the two populations are considered as races, the *Arkansas Race* and the *Lower Mississippi Race*.

A single sample from the Osage, a tributary of the Missouri River, falls extreme in many proportional characters, but is tentatively included in the Arkansas race. No data are available for the sparse material from the upper White River system, where *N. camurus* occurs with *N. galacturus*.

Range.—Upper Arkansas River and tributaries in Arkansas, Missouri, Oklahoma, Kansas and Colorado. Particularly abundant in the Neosho and Illinois Rivers. Rare in Osage River. Tributaries of the Lower Mississippi River in Mississippi and Louisiana.

Habitat.—Cross (1954: 309) states that the species in Kansas prefers moderately fast, clear water, and its abundance in the two Ozark streams, the Neosho and Illinois Rivers, would seem to bear this out. Moore (*in litt.*) however, has indicated that in the more westerly portions of its distribution, the species is found in warmer, more turbid waters. The habitat of the Lower Mississippi race has been described by Bailey and Taylor (1950: 37) in their discussion of *Noturus* (= *Schilbeodes*) *hildebrandi*. The race appears to favor those high gradient streams with clear waters and sandy bottoms, and probably will not be found in more sluggish, flood-plain tributaries.

Etymology.—The name *camurus* is apparently derived from the Latin *camur*, turned inward, in allusion to the blunt snout.

DISPERSAL AND SPECIATION IN THE COMPLEX

From the close relationship of *N. camurus* and *N. galacturus*, it seems obvious that they were derived from a common stock in the distant past. This stock was presumably divided into eastern and western portions, and the two species evolved (see Fig. 3).

Probably *N. camurus* was at one time far more widely distributed than at present, as indicated by the type locality in eastern Colorado, far west of the nearest recent record, and perhaps by the specimens in the White drainage, which may be remnants of a population which has been unable to meet competition successfully. The presence of the Lower Mississippi race may be evidence of a former occupation of much of the lower Mississippi Valley. It seems that the range of the species is contracting at present, and that the southwestern Ozark region is its stronghold. The precise competitive status of the Lower Mississippi race is too poorly known to permit speculation, but where it is found, the species seems to flourish.

N. galacturus probably differentiated in the Tennessee system, becoming adapted to the cool, mountain waters of the uplands. At a comparatively recent date, possibly when glacial effects brought about the presence of cool connections to the Arkansas, White and St. Francis systems, the species crossed the Mississippi and became established in cooler waters to the west. If it was ever present in the Arkansas, there is no longer any evidence, but it is possible that the

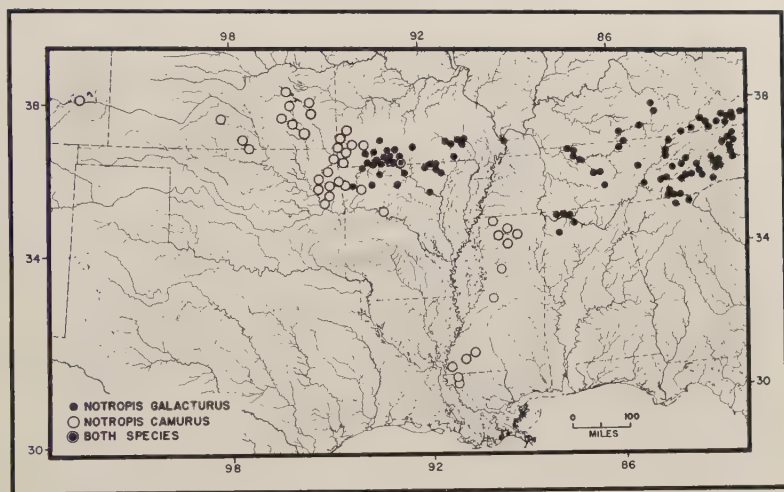


Fig. 3.—Distribution of collections examined of *Notropis galacturus* and *N. camurus*. Records of Ross and Perkins (1959) from the upper Kanawha system are not shown. Dotted line at right marks part of the divide between Tennessee and Atlantic coastal drainages.

warming following the last glacial period has caused a more extensive range to shrink, until it became confined to the faster, cooler portions of the White and St. Francis. That connections may be possible even at present between the populations east and west of the Mississippi is indicated by the collection of *N. galacturus* supposedly taken at Wyatt, Missouri, almost halfway between the two ranges, but much nearer the mouth of the Tennessee than that of the White.

The occurrence of *N. galacturus* in headwater tributaries of the Savannah and Santee systems is doubtless due to stream piracy across the Appalachian divide from Tennessee River tributaries. Ross and Perkins (1959) have recently reported the species from the upper New River in Virginia (Kanawha system). This is apparently due to piracy involving the New and upper Tennessee tributaries, both to the west of the east-west divide.

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Mycological Notes II.¹ New Taxa, Synonyms, and Records²

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ABSTRACT: The following items are included in this paper: 1) Three specimens of *Perichaena microspora* Penz. & List. ap. Penz. from the southern U. S. are discussed and the specific description is amended. This apparently represents the first published record of this species for the western hemisphere. (2) *Lojkania cynodonifolii* [sic] Bat. is relegated to synonymy under *Dimeriella erysipheoides* (Ell. & Ev.) Farr. The reasons for this step, as well as some details explaining the taxonomic background of *Dimeriella erysipheoides*, are presented. 3) The following new fungi are described: *Corynespora elaeidicola* Ell. var. *cercosporioides* Farr on *Heliconia curtispatha* Ped. leaves from Panama; *Peltaster intermedius* Farr on *Ananas comosus* (L.) Merr. leaves from Cambodia; and *Didymella minuta* Farr on *Sesamum indicum* L. leaves from Cambodia. 4) *Cylindrosporium sesami* Hansf., causing a leaf spot disease on sesame, is reported, apparently for the first time, from Asia. 5) New localities, both in Asia, are given for two species of *Cercospora*, *C. melastomobia* Yam. and *C. helianthicola* Chupp and Viég.

PERICHAENA MICROSPORA IN THE WESTERN HEMISPHERE

Perichaena microspora Penz. & List. ap. Penz. was described from Java and Ceylon (Penzig, 1898) and, if included in a major monograph (Lister, 1925; Macbride and Martin, 1934; Hagelstein, 1944), is listed only from these two localities. In a recent publication (Farr, 1959) this species was reported from Africa. (The African collection, gathered by O. F. Cook in Liberia in 1894, is actually four years older than the type specimen, but apparently was overlooked or neglected until 1959.)

At the annual foray of the Mycological Society of America in August, 1960, *Perichaena microspora* was found in Louisiana by George W. Martin and by me. The two specimens were independently collected in the same locality, West Feliciana Parish, Audubon State Park, and each consisted of several small plasmodiocarps on dead needles of *Pinus taeda* L.

¹ The first article of this series appeared in *Mycopathologia et Mycologia Applicata* 12:283-288. 25 May, 1960.

² My thanks are due to C. R. Benjamin and J. A. Stevenson for constructive criticism regarding the manuscript; G. W. Martin for contributing slides of *Perichaena microspora* and helpful comments about this species; C. G. Shaw for the loan of *Lojkania cynodonifolii* type material; R. G. Orellana for providing named herbarium material and cultures of *Cylindrosporium sesami*; and E. K. Cash for checking the Latin diagnoses.

These gatherings were initially believed to represent the first finds of this species in the western hemisphere, but recently Professor Martin unearthed an earlier collection made by Dr. Erdman West near Gainesville, Florida, in July, 1950, and deposited in part in the herbarium of the State University of Iowa. A slide of this material is in the National Fungus Collections. Dr. West did not publish on this collection and has kindly given me permission to do so in this note.

The Louisiana specimens are deposited in the herbaria of the State University of Iowa (SUI) and the National Fungus Collections (NFC) respectively. The latter specimen (NFC no. 71645) is the only collection I saw in habit and it agrees in external (as well as microscopic) characteristics with the diagnosis and Lister's excellent illustration (1925, pl. 185). The capillitium is studded with delicate spines and in part prominently constricted at regular intervals so as to give a beaded appearance under oil immersion. The non-beaded portions display frequent irregular expansions and a consequently fluctuating diameter of 1.5-5 (mostly 2-3.5) μ (Fig. 1). Professor Martin reports fine ridges present in addition to the spines in parts of his material (personal communication). These ridges could also be seen in the Florida specimen. The capillitium of the latter, densely covered with spines to 2 μ long, is hardly at all constricted and has a nearly uniform diameter of ca. 2 μ , sometimes conspicuously swollen at the axils.

The description furnished by Lister (1925), though otherwise excellent, is rather limited with respect to the capillitium. It depicts the latter as "marked with minute spines, regularly constricted at intervals of 1 to 2 μ ." Petch (1910: 369) mentions, in addition, "frequent irregular expansions at the axils," and also refers to the beaded appearance of the threads. These descriptions, however, are now somewhat inadequate, since they fail to include certain variations encountered in the American fruitings. In order to present a more complete picture it seems desirable, therefore, to emend that part of the species description dealing with the capillitium, as follows:

capillitium a loose network of branching threads, yellowish-pink in mass, almost colorless when mounted, densely covered with delicate spines up to 2 μ long, and sometimes in part with fine ridges; threads almost even to torulose, of a nearly uniform diameter of 1.5-2 μ and with nodular enlargements at the axils, or sometimes of irregular diameter (1.5-5 μ) throughout.

The spores of all three collections are minutely spinulose and measure 6.5-8.5 μ diam.

Although *P. microspora* is brightly colored and not one of the most minute Myxomycetes, its elusiveness is understandable. The scattered fructifications are more or less buried in forest litter and thus frequently concealed from the collector's view. A more intense search may reveal the species to be more common and of wider distribution than we believe it to be at present.

LOJKANIA CYNODONIFOLII [sic] BATISTA, A SYNONYM

Recently (1960) Batista described a new species of the previously monotypic genus *Lojkania* Rehm, *L. cynodonifolii* Bat., ap. Bat. & Peres. The type of this species, labelled "*Dimerosporium erysipheoides* Ell. and Ev.", was collected on *Cynodon dactylon* (L.) Pers. by B. C. Tharp at Texarkana, Texas, 16 October, 1915. It is deposited in the herbarium of the State University of Washington.

At nearly the same time as Batista's publication, I published the new combination *Dimeriella erysipheoides* (Ell. & Ev.) Farr based on type material of *Dimerosporium erysipheoides* Ell. & Ev. and a Cambodian collection on the same host (Farr, 1960).

The genus *Dimerosporium* Fckl. is no longer valid since its type, *D. abjectum* (Wallr.) Fckl. is a synonym of *Asterina veronicae* (Lib.) Cke. (Stevens and Ryan, 1939:50). The type of *Dimerosporium erysipheoides*, however, was found to be not an *Asterina*, but rather to represent a distinct species of the genus *Dimeriella* Speg. (Meliolaceae or Sphaeriaceae) and hence was transferred there. Spegazzini (1908:12) segregated *Dimeriella* from *Dimerosporium* by the following statement: "Genus e *Dimerosporio* excerptum, species peritheciis subglobosis astomis setulosis sporis hyalinis donatas sistens."

The genus *Lojkania*, described by Rehm in 1905, apparently differs from *Dimeriella* chiefly in having dark spores and glabrous perithecia. In Batista's description and illustration the spores of *Lojkania cynodonifolii* are olivaceous-brown and the perithecia glabrous, but careful scrutiny of his type specimen reveals a few scattered appendages on the perithecia; the spores, furthermore, at maturity are not brown. Their subhyaline to greenish color appears to be due to the densely granular contents. The perithecial appendages are scarce and sometimes poorly developed, and hence very inconspicuous. The well-formed ones are dark brown and wider than the hyphae, with a more or less bilobed apex. Except for being less numerous, the setae correspond well with those of Ellis and Everhart's (1888) diagnosis of *Dimerosporium erysipheoides*, which reads "[perithecia] surrounded below with 15-20 short spreading appendages $30-40 \times 3$, mostly 1-3-septate, brown and imperfectly bilobate at their extremities." They also appear identical with those of the Cambodian material. The measurements as well as the habit and macroscopic appearance of the Ellis and Everhart type, the Cambodian specimen, and Batista's type of *Lojkania cynodonifolii* agree closely. Thus it can be reasonably asserted that all the material cited and discussed above is of one and the same species and belongs in the genus *Dimeriella*. *Lojkania cynodonifolii* Batista, therefore, becomes a synonym of *Dimeriella erysipheoides* (Ell. & Ev.) Farr.

CORYNESPORA ON HELICONIA

A collection of leaves of *Heliconia curtispatha* Petersen from Panama was found to be infected with a species of *Corynespora*

Güssow (Dematiaceae). This fungus genus has apparently not previously been reported from the Musaceae. The fungus is widely distributed over extensive light brown blotches which, on the upper leaf surface, have a dark brown border and are sometimes surrounded by a bright yellow halo. Whether the *Corynespora* causes the spots or is merely a secondary invader cannot be established at this time.

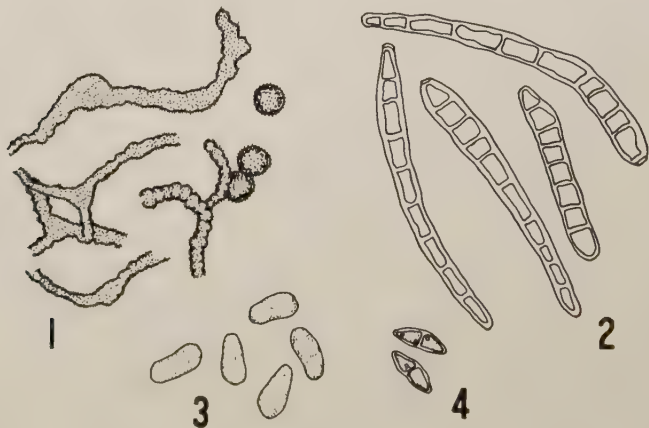
This hyphomycete strongly suggests a *Cercospora* because of its narrow conidia, but their general shape and the greater prominence of the walls seem more characteristic of *Corynespora*. The organism appears to be on the border line between the two genera. Other particulars of this fungus include the presence of light to dark brown stromata; nearly straight to strongly geniculate, fascicled conidiophores mostly between 105μ and 275μ long and $3-5\mu$ in diameter; and pale brown, sometimes guttulate conidia measuring $40-85\mu$ (av. 67) in length and $5-7\mu$ (8) in width. It comports with the description and illustration of *Corynespora elaeidicola* Ellis (1960:24, Fig. 16) in all respects except in the possession of much longer conidiophores and large numbers of conidia that are attenuated rather than blunt at the apex, as shown in Ellis' drawing; furthermore, *C. elaeidicola* so far has been reported only on the Palmaceae. The fungus on the *Heliconia* is therefore described here as a variety of *Corynespora elaeidicola*.

Corynespora elaeidicola Ellis var. ***cercosporioides*** var. nov.

Fig. 2

A typo differt conidiophoris longis, conidiis ad apicem saepe attenuatis.

Type.—On leaves of *Heliconia curtispatha* Petersen, Canal Zone, Panama; ex E. P. Imle s.n., Dec. 1959. (NFC 71646).



Figs. 1-4—1. *Perichaena microspora* Penz. & List., capillitium and spores; $\times 500$. (NFC 71645). 2. *Corynespora elaeidicola* Ellis var. *cercosporioides* Farr, spores; $\times 620$. (Type). 3. *Peltaster intermedius* Farr, spores $\times 600$. (Type). 4. *Didymella minuta* Farr, $\times 635$. (Type).

A NEW SPECIES OF PELTASTER

Two specimens of pineapple leaves received from Cambodia exhibited a superficial black mold with mycelium resembling that of *Asterinella stuhlmanni* (P. Henn.) Theiss. and possibly belonging to the conidial state of the same. Since, however, no ascogenous fruit bodies were present and apparently no pycnidial state is known for the *Asterinella*, the fungus on the Cambodian material is here described as a new species of *Peltaster* (Leptostromataceae).

A tabular comparison (Table I) of this fungus with the three previously described species of *Peltaster* (*P. hedyotidis* Sydow, 1917: 261; *P. guraniae* Toro ap. Chardon and Toro, 1934: 232; and *P. byrsonimae* Hansford, 1955: 83) shows that the conidia of the new

TABLE I.—A comparison of the species of *Peltaster*

Species	Diameter of fruit bodies	Size of spores	Habit
<i>P. Hedyotidis</i> Syd.	110-150 μ	8-10 $\times$ 4-5 μ	hypophyllous
<i>P. byrsonimae</i> Hansf.	to 180 μ	14-17 $\times$ 3-3.5 μ	hypophyllous
<i>P. guraniae</i> Toro ap. Chardon & Toro	331-486 $\times$ 57-80 μ	6-9 $\times$ 2-3 μ	hypophyllous
<i>P. intermedius</i> sp. nov.	150-220 μ	10-13 $\times$ 5 μ	epiphyllous or hypophyllous

species are wider than those of all other species except *P. hedyotidis*, but the range of their length falls between that of *P. hedyotidis* and that of the other two species. The fruit bodies are larger than those of *P. hedyotidis*, smaller and of a different shape than those of *P. guraniae*, and apparently overlapping those of *P. byrsonimae* in diameter. The new species is, furthermore, the only one so far reported on a monocot.

Peltaster intermedius sp. nov.

Fig. 3

Mycelium ex hyphis sinuoso-reticulatis, ramosis, exhyphopodiatis, olivaceis vel atro-brunneis, indistincte septatis, 2-4 μ diam. compositum; pycnidia singula vel connata, in hyphis mycelii evoluta, 150-220 μ diam., orbiculata, scutata, poro centrali vel eccentrici dehiscens; paries superior radiatus, margine plus minusve fimbriatus, ex hyphis brunneis compositus; conidia hyalina, continua, 1-3-guttulata, oblonga vel elliptica, 10-13 $\times$ 5 μ , utrinque rotundata.

Mycelium superficial, wavy-reticulate, branching, generally asterinaceous in appearance but without hyphopodia, olivaceous to deep brown, darkest near the fruit bodies or fruit body initials, indistinctly septate, 2-4 μ diam.; pycnidia single or several fused, 150-220 μ diam., covered by a network of mycelium, orbicular, scutate, dark brown with a more or less fimbriate margin and a cen-

tral or eccentric pore; conidia hyaline, continuous, 1-3-guttulate, $10-13 \times 5\mu$, oblong to elliptical, sometimes shoe-shaped, the ends rounded.

Holotype.—On leaves of *Ananas comosus* (L.) Merr., Chamcar Krauch, Cambodia, *Litzenberger* 314, 30 Oct. 1959. (NFC 71647).

Paratype.—On the same host from the same locality, *Litzenberger* 60, 27 Aug. 1958. (NFC 71648).

A number of the conidia, when mounted in lactophenol, appeared one- or two-septate, but examination under oil immersion indicated that this was due to the arrangement of the droplets which are sometimes very close together and separated only by a thin strand of cytoplasm. In an aqueous phloxine mount, the droplets remain unstained, but are not as sharply delimited as in lactophenol.

DIDYMELLA ON SESAME

A minute species of *Didymella* (Sphaeriaceae or Pleosporaceae) was found scattered on some leaf spots of two *Sesamum indicum* L. specimens from Cambodia. The spots were of irregular shape, pale brown with concentric lines and dark brown borders, and resembled those caused by *Alternaria* sp. Dematiaceous conidiophores and several types of detached dematiaceous spores were discernible on the leaf surface. Whether the *Didymella* was parasitic or saprophytic could not be ascertained from the material and information on hand; possibly it represented the perfect stage associated with one of the Dematiaceae.

Evidently no members of the genus *Didymella* have been reported from any species of the Pedaliaceae. The organism on the sesame leaves varies from most *Didymella* reported from dead leaves of various plants primarily in its conspicuously small perithecia. From *D. exigua* (Niessl) Sacc. and *D. pedicularidis* v. Arx, with both of which it essentially agrees in perithecial, ascus, and ascospore measurements, it differs in its non-constricted ascospores.³ The perithecial wall cells of *D. exigua*, furthermore, are "at times roughened by scattered thick-walled, protruding cells, tomentose" (Barr, 1959) while those of the sesame fungus appear consistently thin and smooth. The latter is therefore described as a new species.

Didymella minuta sp. nov.

Fig. 4

Perithecia erumpentia, nigra, membranacea, globosa, ostiolata, c. $70-90\mu$ diam.; asci cylindranei vel elliptici, 8-sporei, bitunicati, $40-50 \times 10-13\mu$; paraphyses filiformes; ascosporae 1-septatae, hyalinae, fusiformae, rectae vel leniter curvatae, non vel vix constrictae, guttulae, $11-15 \times 3-4.5\mu$.

Perithecia erumpent, black, membranous, globose, ostiolate, c. $70-90\mu$ diam.

³ Barr (1959) describes the ascospores of *D. pedicularidis* as not constricted. V. Arx (1950), on the other hand, states that they are more or less constricted; in his sketch they appear definitely constricted, and not so pronouncedly fusiform as those of the sesame fungus.

at maturity; ostiole a roundish pore, c. 20μ diam.; perithecial wall composed of smooth, variously-shaped cells $5-8\mu$ diam., those around the ostiole often being darker; asci cylindrical or elliptical, 8-spored, bitunicate, $40-50 \times 10-13\mu$; paraphyses filiform; ascospores 1-septate, greenish-hyaline, spindle-shaped, straight or slightly curved, not or scarcely constricted at the septum, guttulate, $11-15 \times 3-4.5\mu$.

Holotype.—On leaves of *Sesamum indicum* L., Kompong Cham, Cambodia, *Litzenberger* 12, 1958. (NFC 71649).

Paratype.—On same host, Reilin, Cambodia, *Litzenberger* 324, 1959. (NFC 71650).

CYLINDROSPORIUM SESAMI HANSFORD FROM CAMBODIA

This fungus was described as the causal organism of a leaf spot disease on *Sesamum indicum* L. in Uganda (Hansford, 1938, p. 47). Recently this fungus was noted for the first time in the United States (Anonymous, 1960; Orellana, 1961).

The same organism has now been found on sesame leaves from Cambodia (Prek Leap Sta., *Litzenberger* 13, 10 July 1958. NFC 71651) and the present note apparently constitutes the first report from Asia. The possibility exists, however, that an earlier report of "*Cercospora* sp." from Malaya (Thompson and Johnston, 1953:29) may refer to the same fungus.

The Cambodian collection agrees well in its measurements with those stated in the species diagnosis of *Cylindrosporium sesami*; it also is identical in microscopic features and in shape of the leaf spots with named American material of this species. The color of the spots differs, however, in being a uniform, opaque gray-brown in the Cambodian material, and a more translucent light-brown in the American specimen. This may be due to a possible association with *Alternaria* sp. (The Cambodian specimen was labelled "*Alternaria* leaf spot," but only an abundance of the *Cylindrosporium* was detected on the dry leaves.)

NEW LOCALITY RECORDS FOR TWO SPECIES OF CERCOSPORA

Cercospora melastomobia Yamamoto and *C. helianthicola* Chupp & Viégas were listed by Chupp (1953) as known only from their type localities (Formosa and Brazil, respectively) and I could find no additional record of either species in subsequent literature.

C. melastomobia was found on leaves of *Melastoma candidum* D. Don. from Hong King Island, *N.L.H. Krauss* 344 and probably 345 (the latter poor material), 30 Apr. 1958. (NFC 71652 and 71653.) The fungus on the former specimen corresponds well with type material of the species.

Some dried leaves of *Helianthus annuus* L. from Cambodia (Siem-reap, *Litzenberger* 377, 18 Aug. 1960. NFC 71654) were infected with *Cercospora helianthicola*. In Chupp's monograph, this species is distinguished from the other *Cercosporae* on *Helianthus* by the

possession of hyaline, acicular conidia; and the Cambodian material is in close agreement with the characterization and illustration of *C. helianthicola*.

The type specimens of the new taxa described in this paper are deposited in the National Fungus Collections, Plant Industry Station, Beltsville, Maryland (NFC).

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Studies on the Biology of *Philophthalmus gralli* Mathis and Leger, 1910 (Trematoda: Digenea)¹

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ABSTRACT: The adult of *Philophthalmus gralli* occurs in the orbit of wild birds and has been obtained experimentally in chicks. Rodents were refractory to infection by the oral route. *Goniobasis* spp. and *Pleurocera acuta* serve as molluscan hosts. The miracidium penetrates the snail only far enough to release a single redia. It localizes in the heart and produces daughter rediae which migrate to the digestive gland and produce megalurous cercariae. Cercariae escape and encyst on the exoskeleton of arthropods which are eaten by the definitive host, in which the worms migrate to the eye by way of the nasolacrimal duct. Factors concerned with such migration are considered and all stages in the life history are described. The family Ommatobrephidae is reduced to synonymy with the Philophthalmidae and the species *Philophthalmus nyrocae* to synonymy with *Philophthalmus gralli*.

Studies on the life histories of digenetic trematodes has yielded information that is basic to the interpretation of affinities between families and more inclusive taxa (La Rue, 1957). The development of the cercarial stage and its type have been particularly useful in postulating relationships that may not be readily apparent from morphology of the adult alone. Such studies have shown that each family has a common cercarial type and that when the life history of one species is determined, that of other cercariae of the same type may be expected to follow a similar pattern.

In his monographic study, Sewell (1922) followed Cort (1915) in recognizing a Megalura Group of cercariae based on the American fresh water species, *Cercaria megalura*. After Stunkard and Cable (1932) found that a very similar marine species was the larva of *Parorchis acanthus*, a cloacal parasite of birds, their procedure was used in this laboratory 25 years ago in attempts to determine the life history of a fresh water species. Although metacercariae were fed to a variety of vertebrates, the adult was not found for a reason that is now apparent: failure to examine the ocular orbit. The clue to that oversight came much later in this laboratory when Cable, Connor and Balling (1960) decided that Travassos (1918) probably was correct in placing *Parorchis* and *Philophthalmus* in a separate family, the Philophthalmidae, rather than in the Echinostomatidae of which those genera were generally regarded to be aberrant representatives. It fol-

¹ Based on a thesis prepared under the direction of Prof. R. M. Cable and submitted in partial fulfillment of the requirements for the Ph.D. degree, Purdue University. I am especially indebted to my colleague, Frank M. Fisher, Jr., who shared in the early phases of this study and later aided in the collection of naturally infected mollusks and birds.

lowed then that the adult of the fresh water cercaria might be a species of *Philophthalmus* occurring in the orbit of birds. Such proved to be the case and preliminary studies were reported in a brief note (Fisher and West, 1958). The present paper reports the life history of the parasite in detail and certain other aspects of its biology.

METHODS

Two species of naturally infected snails were used as a source of larval trematodes: *Goniobasis* sp. from Fourteen Mile Creek in southern Indiana and *Pleurocera acuta* from the Tippecanoe River near Battle Ground, Indiana. Infected snails were detected by isolation in finger bowls of water and maintained for periods of several months in tanks of shallow, well-aerated water containing a thin layer of silt. Small amounts of 10-52-17 fertilizer were added to promote growth of diatoms and other organisms essential to nutrition of the snails. Such growth was further stimulated by 15-16 hours of artificial light per day and by maintaining a water temperature of 25°-30° C. with the aid of immersion heaters.

To obtain metacercariae for feeding experiments, infected snails were isolated in finger bowls of water until cercariae emerged and encysted on the glass. The cysts were then scraped loose and fed to chicks, hamsters, rats, mice, guinea pigs and rabbits which were either sacrificed to study migration of the young worms or, if susceptible to infection, maintained as a source of adults. Although miracidia can be obtained in washings from the orbit of infected birds, adult worms usually were removed with a pipette and placed in water or 0.45% NaCl in which eggs were laid in large numbers. Thereafter, the worms were returned to the orbit of the host to be used again if needed. The eggs hatched in a short time and the miracidia were used to study their morphology or for infecting snails which were placed in small stender dishes of water to which various numbers of miracidia were added. Following exposure, the snails were handled as described above for naturally infected ones; some were examined at intervals to observe larval development and others isolated periodically until cercariae emerged.

All stages of the parasite were studied alive in sealed preparations and as whole mounts after fixation in A.F.A. or Bouin's fluid and staining with Semichon's carmine or Harris' hematoxylin. In addition, the silver nitrate technic of Lynch (1933) was used with all stages. Serial sections were prepared after fixation in hot Bouin's fluid and were stained with Harris' hematoxylin and eosin. Unless otherwise stated, drawings were made by microprojection with details added freehand. All measurements are in millimeters unless otherwise indicated.

Worms maintained in vitro were incubated at 38° C in a medium consisting of one part fresh egg albumin, two parts Tyrode's balanced salt solution, three parts distilled water, two drops fresh egg yolk, 200 units/ml. Penicillin-G potassium and 1 mg/ml streptomycin sulfate.

Methods used to investigate possible factors influencing migration in the definitive host are described with the results of such experiments.

OBSERVATIONS AND DISCUSSION

EXPERIMENTAL DETERMINATION OF THE LIFE HISTORY

The first part of the life history was demonstrated experimentally by rearing the adult parasite in the orbit of chickens which were fed metacercariae. The cercariae were from naturally infected snails. The larvae normally encyst on the exoskeleton of arthropods, especially crayfishes, but cysts used in infection experiments were scraped from finger bowls. Many of the worms probably were injured in that process because some chickens did not become infected and others harbored fewer worms than the number of metacercariae fed. It is also likely that some of those that were not injured failed to reach the orbit for other reasons. The largest number of worms found in a naturally infected bird was 20 in a green heron, *Butorides virescens*; they were of various ages to judge from their sizes in contrast to the usually very uniform size of worms from chickens fed a single lot of metacercariae.

The life history was further elucidated experimentally by infecting snails with miracidia from worms reared in chicks. Many snails were thus exposed and sacrificed at intervals to study larval development of the parasite, but 15 *Goniobasis* sp. and 10 *Pleurocera acuta* were maintained and examined periodically for emerging cercariae. Six *P. acuta* survived and 3 shed cercariae at the end of 4 months. When *Goniobasis* sp. did not do so by the end of the 6th month, the 3 surviving individuals were sacrificed; one contained daughter rediae and a few apparently mature cercariae.

Because it is difficult to maintain prosobranch snails in a state of good nutrition in the laboratory, it is possible that under more favorable conditions, infected snails might shed cercariae within less time. Furthermore, it may be that the larger body of *P. acuta* favors the development of rediae and cercariae over the smaller *Goniobasis* sp. which, in natural infections, shed much smaller numbers of cercariae than did *P. acuta*.

Experimental demonstration of the life history was completed by permitting cercariae from experimentally infected *P. acuta* to encyst and feeding the metacercariae back to a chicken which had provided miracidia used to infect the snails, thus obtaining adult worms for the 2nd time from a single host.

TAXONOMY

Dawes (1956) included in the Philophthalmidae the genera *Philophthalmus* and *Pygorchis* but not *Parorchis* and *Echinostephilla* which he treated as isolated genera of the Echinostomatidae. Yamaguti (1958) recognized the Philophthalmidae to include the subfamilies Parorchinae Lal, 1936, Philophthalminae Looss, 1899, and

three new ones: Cloacitreminae, Echinostephillinae and Skrjabinovertinae. Not only does each of the new subfamilies contain a single genus but, as Ching (1960) pointed out, *Skrjabinovertis* is a synonym of *Echinostephilla* according to the Zoological Record for 1953. Recently, Dubois and Mahon (1959) transferred the genus *Parorchis* to the family Ommatobrephidae Poche, 1926, which previously had contained only the genotype. A comparison of *Ommatobrephus* with philophthalmid genera reveals no differences that justify recognition of the Ommatobrephidae. That family accordingly is reduced to synonymy with Philophthalmidae which has priority.

Identification of the present species is complicated by the fact that at least 21 species of *Philophthalmus* have been named, including the following which were not listed by Alicata and Ching (1960): *P. posaviniensis* and *P. cupensis* described by Richter, Varzic and Aleraj (1953) and *P. gnedini* Trofimov as listed by Tret'iakova (1948). The differences between some of those species are no greater than the writer observed as variation within the present one. Some of his specimens bear a striking resemblance to *P. nocturnus* but all differ from that species as described by Looss (1907) in having a smaller oral sucker and pharynx, armed cirrus and much less saccate excretory vesicle. Because there is closer agreement with *P. gralli* Mathis and Leger (1910), as redescribed by Sugimoto (1928), the writer's material is identified as that species. A single specimen described by Yamaguti (1934) as *P. nyrocae* differs from *P. gralli* only in the absence of an eye spot in the miracidium. In the present study, an occasional adult worm, although gravid with eggs, contained none in which a miracidium with an eye spot had developed. Because Yamaguti may have been dealing with such a specimen and because such similar trematodes normally produce miracidia that are very much alike, *P. nyrocae* is reduced to synonymy with *P. gralli*. More than likely, other synonymy exists among species of *Philophthalmus* that have been erected on the basis of the size and shape of the testes, and the extent of the vitellaria and cirrus sac which the author found to vary considerably in the present species. For that reason, a critical comparison of megalurous cercariae and correlation with their adults is an important, if not indeed indispensable approach to the problem of speciation in the genus *Philophthalmus*.

REDESCRIPTION OF THE ADULT

Philophthalmus gralli Mathis and Leger, 1910 (Figs. 1-2)

Description (based on numerous specimens obtained from both natural infections in wild birds and experimentally infected chicks; measurements from stained whole mounts).—Elongate, medium-sized distomes with the characters of the genus. Body fusiform with rounded ends in living worms, more lanceolate with hind body expanded in flattened specimens. Cuticle with imbedded spines 0.01 long, confined to ventrolateral regions of fore body, difficult to see except in sections.

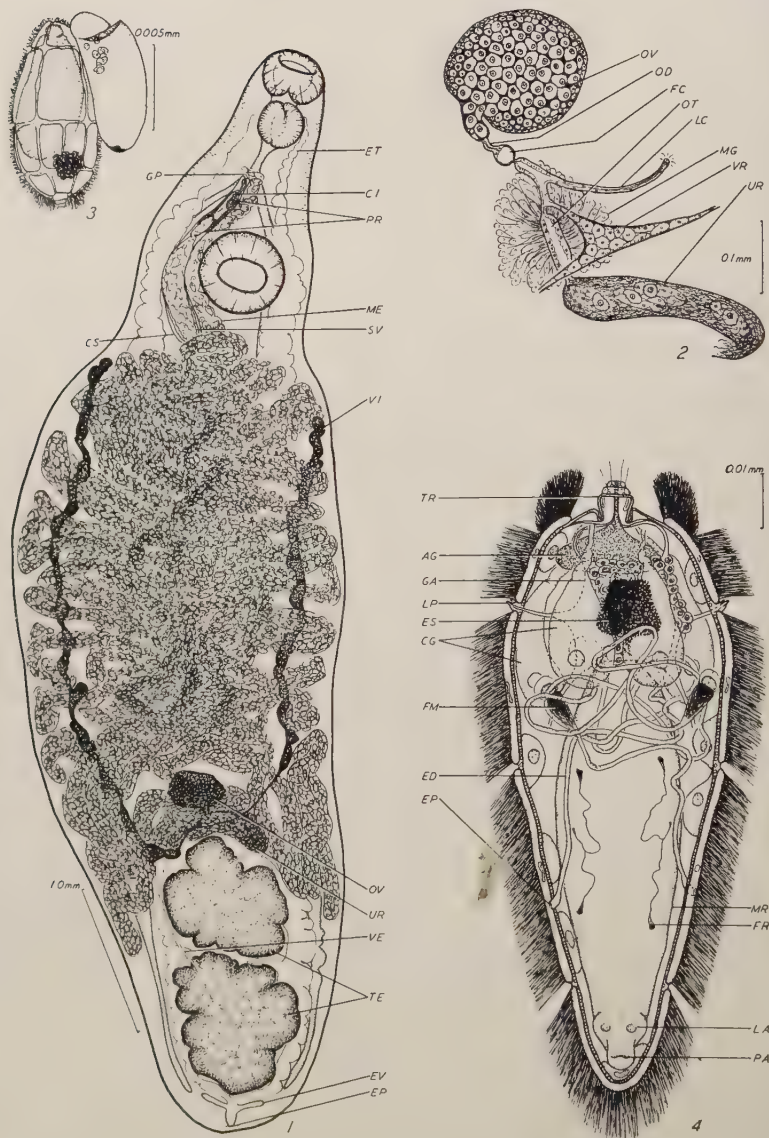
Mature specimens 3.42-8.36 long; 0.67-2.07 in maximum width. Ventral sucker in anterior fourth of body, spherical, 0.43-0.70 in diameter. Oral sucker terminal, 0.20-0.37 long by 0.21-0.47 wide; mouth slightly subterminal, prepharynx very short and wide; pharynx massive, 0.19-0.35 long, 0.17-0.31 wide, wider in sagittal than in frontal plane, its lumen a narrow dorsoventral slit in cross-section. Esophagus usually a little shorter than pharynx, intestinal bifurcation about midway between pharynx and ventral sucker; ceca narrow, reaching posterior end of body, sometimes slightly sinuous or with shallow lateral diverticula.

Testes tandem, entire to distinctly lobed; anterior testis 0.27-1.10 long, 0.25-0.87 wide; posterior testis 0.25-1.01 by 0.21-0.89. Vasa efferentia leave ventral surface of testes near their anterolateral margins and unite before reaching cirrus sac, forming a vas deferens averaging 0.93 long. Cirrus sac dorsal to, or to either side of ventral sucker, slender, 0.83-1.70 long, 0.09-0.32 wide, its extent variable but always overreaching ventral sucker; seminal vesicle sometimes entirely posterior to that sucker. Pars prostatica tubular, averaging 0.19 long; cirrus large when everted, with conical spines 0.005-0.01 long. Genital atrium very shallow if present, the sex openings apparently being separate with female immediately anterior to male.

Ovary submedian, a short distance anterior to testes, circular to oblong in outline, 0.12-0.37 in diameter; with a tail-like extension joining the short, narrow oviduct which enlarges to form fertilization chamber about 0.03 in diameter. Beyond chamber, oviduct is joined first by Laurer's canal which opens to outside dorsally, then by duct of vitelline reservoir. From it vitelline ducts extend laterally ventral to ceca, joining posterior limits of tubular to almost follicular vitellaria ventrolateral to ceca. Anterior extent of vitellaria varying from a level overlapping posterior end of cirrus sac by 0.27 to one not attaining the level of that structure by 0.70; average extent 0.17 posterior to cirrus sac. Mehlis' gland, oötype and proximal portion of uterus posterior to ovary. Uterine coils extensive, occupying width of body from testes almost to ventral sucker, sometimes overlapping anterior testis ventrally and flanking male gonads to midlevel of posterior testis. Metraterm begins posterior to ventral sucker as muscular coils surrounded by unicellular glands, and extends anteriorly parallel to cirrus sac. Eggs numerous; miracidia fully developed, each with double eye spot and containing a redia.

Excretory pore posterior, slightly dorsal; vesicle short, triangular to T-shaped in outline with a very short anterior stem receiving voluminous ascending excretory trunks which extend to sides of pharynx before turning posteriorly as narrower canals; receiving secondary tubes at about level of ventral sucker. Excretory pattern not completely determined but with more flame cells than in cercaria.

Hosts.—Experimental, chicken (*Gallus gallus domesticus*); Natural, green heron (*Butorides virescens*), belted kingfisher (*Megaceryle alcyon alcyon*), bittern (*Botaurus lentiginosus*) and grackle (*Quiscalus quiscula*).



Figs. 1-4.—1. Adult *Philophthalmus gralli* from naturally infected Kingfisher (*Megaceryle alcyon alcyon*), ventral view. 2. Female complex (free-hand). 3. Miracidium and egg shell, fixed in AgNO_3 (free-hand). 4. Miracidium enlarged to show details (free-hand).

Site.—Orbit at exit of lacrimal duct.

Locality.—Indiana, United States.

Other hosts and localities.—duck (*Anas boschas domestica*), in Formosa; chicken (*Gallus gallus domesticus*), in Indo-China; duck (*Nyroca ferina ferina*), in Japan.

Adult worms in the orbit of experimentally infected chicks cause little noticeable irritation even when the parasites are large or several are present. A tolerance of the parasites may develop gradually as an uninfected bird shows evidence of discomfort for a while when an adult worm from another bird is placed directly in the orbit. The retracted nictitating membrane of infected birds is somewhat more conspicuous than normal and the posterior ends of large worms may project from beneath its free edge.

When removed and placed in 0.85% NaCl or water at room temperature, the worms are very active and frequently protrude the long cirrus. Under these conditions, worms at least 6 weeks of age lay large numbers of eggs which hatch promptly. The distended excretory system is conspicuous and, being transparent, outlines many of the internal organs which can be seen when live worms are projected on a screen. They and the miracidia thus have been used effectively for class room demonstration. The adults also are unusually favorable for research because they are readily removed, subjected to experimental procedures and returned to the orbit of the same or another host. Because the worms do not leave the orbit after reaching it, a single bird may be used for experimental and control parasites, thus eliminating individual host differences as a variable.

DEVELOPMENT IN THE DEFINITIVE HOST

The gonads and cirrus sac of young worms become evident by the 6th day after the chick is fed metacercariae. Sperm in the testes and sometimes the seminal vesicle and female tract appear by the 14th day and, by the 22nd, the uterine seminal receptacle is distended with them. Eggs are present in the proximal uterine coils

Abbreviations: AG—apical gland; BP—birth pore; BS—body spines; C₁—cystogenous glands, cell type 1; C₂—same, cell type 2; C₃—same, cell type 3; C₄—same, cell type 4; CG—cephalic glands; C1—cirrus; CP—ciliated patch; CS—cirrus sac; ED—excretory duct of miracidium; EP—excretory pore; ES—eye spot; ET—excretory trunk of adult; EV—excretory vesicle; FC—fertilization chamber; FM—flame cell of miracidium; FR—flame cell of mother redia; GA—ganglionic mass; GL—glands of metacercaria; GP—genital pore; LA—lateral adhesive appendage; LC—Laurer's canal; LP—lateral papilla of miracidium; MB—muscle bands of terebratorium; ME—metraterm; MG—Mehlis's gland; MO—mouth of rediae; MR—mother redia; OD—oviduct; OS—oral spines; OT—oötype; OV—ovary; PA—posterior adhesive appendage; PH—pharynx; PO—pores of cephalic gland; PR—pars prostatica; SH—snail heart; SP—sensory papillae; SV—seminal vesicle; TE—testes; TR—terebratorium; UR—uterine seminal receptacle; VE—vas efferens; VI—vitellaria; VR—vitelline reservoir.

by the 14th day and eye spot pigment appears in the developing miracidia about the 31st day but about 35 days are required for the worm to contain eggs that hatch normally and release fully developed miracidia. The adult may persist in the conjunctival sac of the chicken for over 10 months and still contain many eggs in the uterus but it was also observed that the reproductive capacity often was greatly reduced or apparently exhausted in some worms after 75 days.

That the parasite is selective in its growth requirements was demonstrated by subjecting young worms to certain abnormal conditions. Thus, one, taken from the nasal membranes of a hamster infected 19 days earlier, had reproductive organs no further developed than those of a 4-day worm from the orbit of the chick. In the amniotic and yolk sacs of chick embryos, excysted metacercariae developed only about as far in 11 days as they do in the orbit in 3. Finally, 8-day old worms developed no further when removed from the orbit of chicks and maintained in vitro for 30 days.

THE EGG AND MIRACIDIUM

(Figs. 3, 4-7)

The egg is non-operculate and oval with one side slightly flattened. The shell is thin and elastic and has an internal thickening at the small end. When first formed, the shell averages 0.07 by 0.03 and is deep yellow but it attains an average size of 0.11 by 0.05 and becomes pale in color due to stretching as the miracidium develops. When laid by worms placed in 0.85% NaCl, the eggs further enlarge to an average of 0.13 by 0.06 but after hatching, the shell contracts to an average size of 0.09 by 0.04 (Fig. 1). In whole mounts, eggs are noticeably shrunken, fully developed ones in the metraterm averaging 0.08 by 0.04.

When ripe eggs are released from the worm into water or saline, the miracidia become very active and push repeatedly at the large end of the shell until hatching occurs. The lateral papillae apparently do not facilitate that process as Rees (1940) described for the miracidia of *Parorchis acanthus*. Indeed, the cilia beat continuously while the anterior end of the larva is pressed from side to side against the shell until it suddenly ruptures and contracts, forcibly ejecting the miracidium. Although an operculum is not evident, the shell always tears evenly and at the same place so that the large end resembles a cap that remains attached at one point.

Description of the miracidium (measurements from specimens killed in hot 0.2% silver nitrate unless otherwise stated)—oval, 0.10 long by 0.05 wide. Epithelial cells in 4 tiers with nearly always 6, 8, 4 and 2 cells respectively; their nuclei irregularly elongate or stellate. Cells of 1st tier about 0.02 long, triangular with indented base; those of 2nd tier rectangular, averaging 0.03 long; 3rd tier trapezoid, 0.04 long, not always continuing bilateral symmetry of preceeding tiers; 4th tier 0.03 long, capping posterior end of larva. All epithelial

cells with cilia at least 0.01 long in living miracidia; cilia of anterior 3rd of first tier heavier and directed forward. Subepithelium thin, with a few large parenchymal cells scattered beneath a layer of rather evenly spaced circular muscle fibers and fewer scattered longitudinal ones. Two pairs of lateral sensory papillae and 10-12 small circular ciliated patches in space between tiers 1 and 2. Excretory openings posterolateral, between epithelial cells of 3rd tier, usually at about its midlevel. Terebratorium 0.03-0.04 long when protruded, with 4 strong longitudinal muscle bands effecting lateral as well as retracting movements; distal end of terebratorium with 10 papillae, each bearing a sensory bristle. Apical gland filled with large granules, with a syncytial mass containing 4 nuclei at base, and narrow duct opening at tip of terebratorium. Cephalic glands 4, in subdorsal and ventrolateral pairs, difficult to see, dorsal to eye spot and reaching to mid-level of 2nd epithelial cell tier; each gland with 1-3 openings just beneath anterior edge of 1st tier. Large ganglionic mass immediately ventral to the eye spot, with peripheral cells and 6 processes, evidently fiber tracts, 2 extending into terebratorium, 2 to lateral sensory papillae, and 2 posteriorly. Eye spot 0.01-0.02 long, 0.02 wide, each half with indistinct lenticular body. Flame cells 2, large, at mid-level of 2nd epithelial cell tier; their ducts extensively looped at that level, between subdorsal cephalic glands and subepithelium, imbedded in a hyaline mass and expanding to form small terminal ampullae at excretory pores. Contained redia averages 0.08 long by 0.03 wide, occupying most of miracidium posterior to ganglionic mass; excretory pattern of redia 2 [(1)+(1)]; nuclei of pharynx, genital cells and small cement glands leading to 3 posterior appendages visible in living specimens, intestine not evident.

While swimming, the miracidium rotates with the terebratorium telescoped, and is oval in shape with the maximum width at the level of the 2nd tier of epithelial cells (Fig. 4). In water, miracidia swim for 4 to 6 hours during which they become progressively less active. They move toward the source of a beam of light and, upon reaching the edge of the container, may collect there but some immediately swim in the opposite direction. Soon, however, most of them swim about, crossing the beam a few times before again moving with it toward the light source to repeat the swimming pattern. In the presence of the snail, the miracidium may or may not swim at increased speed in a tight circle until it contacts the host and perforates the epidermis with the aid of secretions and the anterior cilia. A crater forms and nearly conceals the penetrating miracidium which, however, does not completely enter the snail's tissues. Instead, the contained redia becomes active and, by pushing the terebratorium to one side, leaves the miracidium within minutes and passes into the lymph spaces of the host. The life cycle therefore differs from that of most digenetic trematodes in lacking a definitive miracidium-sporocyst stage in which germinal multiplication occurs.

FIRST GENERATION REDIAE

(Figs. 8, 9, 11)

Small mother rediae were found in the heart of the snail 3 hours after its exposure to miracidia. Although a few such rediae can be found elsewhere in sections, they complete their development only within the heart and do not leave it. That organ becomes enlarged when several rediae are present. The heart of a snail removed 74 days after exposure to miracidia contained rediae of both the 1st and 2nd generations (Fig. 9). They adhere to the endocardium with the 3 posterior adhesive appendages and may be very difficult to dislodge. The tip of each appendage shows many fine indentations (Fig. 11), the openings of glands which secrete a sticky substance.

After 3 months, the redia may be over 1.0 long and has a subspherical pharynx 0.07 in diameter in stained specimens. Numerous papillae with short filamentous projections are irregularly distributed around the mouth (Fig. 8) and a few are scattered over the body. In silver nitrate-treated specimens, the papillae appear as small circles and the intestinal epithelium is delineated as extremely thin polygonal cells with finely irregular borders. The intestine reaches the lateral appendages and is distended with ingested food. Daughter rediae are numerous and escape through a ventral birth pore just posterior to the pharynx.

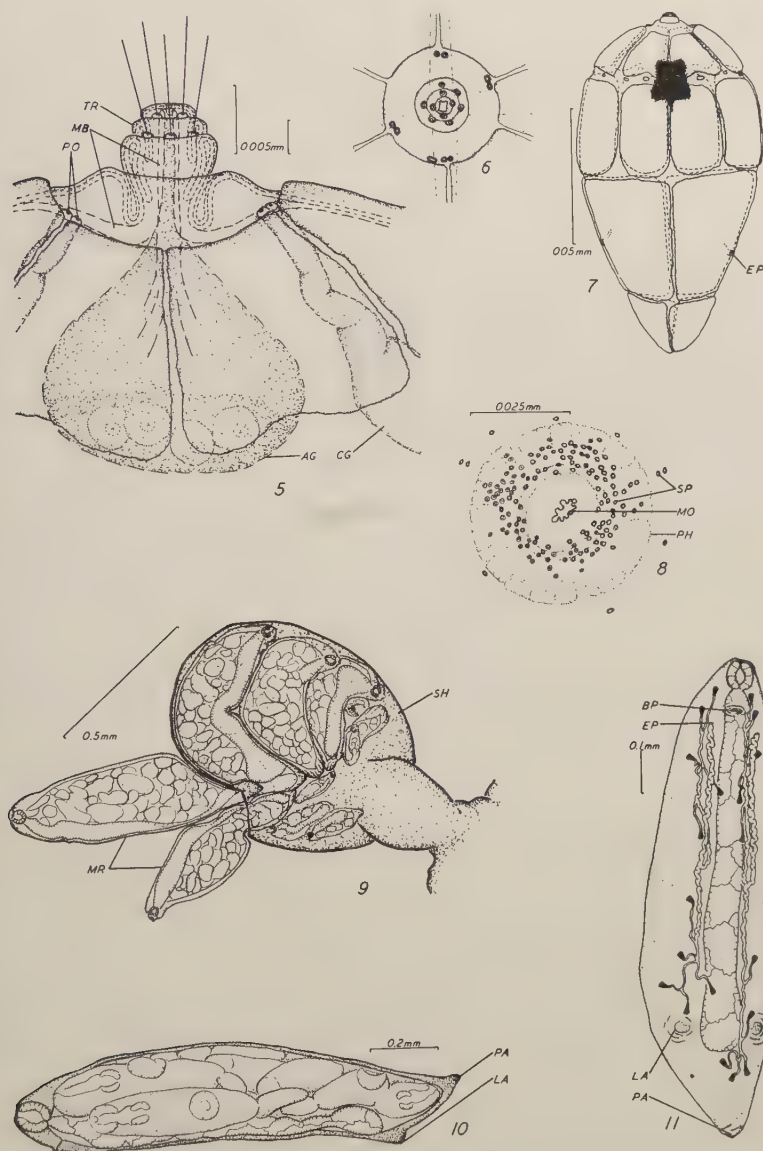
The excretory tubes are tortuous and appear to be imbedded in a hyaline mass loosely adherent to the body wall. Their pores are ventrolateral, just posterior to the birth pore. The flame cell pattern attains a formula of $2[(5) + (5)]$ with any group occasionally lacking one flame cell (Fig. 11). The system is asymmetrical in that the last group extends posteriorly farther on the left side than on the right.

SECOND GENERATION REDIAE

(Figs. 8, 10, 11)

Six weeks after the snail is infected, daughter rediae can be found free in the circulatory passages of the host, especially those of its kidney and digestive gland. With the dissecting microscope, these rediae, and later the cercariae, may be observed in the intact snail by positioning it so that the mantle and gills are visible with strong substage illumination. The rediae then are seen attached by their posterior appendages to the blood vessels and sway back and forth as the blood flows past them. Small rediae were seen there in old infections but by the time that cercariae emerged, mother rediae could no longer be found in the heart.

The digestive gland is the definitive site at which daughter rediae continue their development and produce cercariae. Morphologically, the two redial generations would be difficult to distinguish were it not for their contained brood. Six months after snails are infected, large daughter rediae killed in hot fixative without pressure average 1.59 long and have a subspherical pharynx 0.05 in diameter.



Figs. 5-11.—5. Terebratorium, showing sensory papillae, muscle bands, glands and their openings (freehand). 6. Same, end view (freehand). 7. Epithelial plates of miracidium (freehand). 8. Sensory papillae of rediae, oral region. 9. Mother rediae in snail heart. 10. Daughter redia. 11. Redia, showing excretory system and gut cells (freehand). (Abbreviations as in Figs. 1-4.)

THE CERCARIA
(Figs. 12-31)

Diagnosis (measurements from spontaneously emerging larvae killed in hot A.F.A. fixative).—With characters of the Megalura Group Sewell, 1922. Body 0.54-0.67 long, 0.12-0.13 in maximum width slightly anterior to ventral sucker, indented at level of that sucker. Tail 0.93-1.14 long, 0.04-0.05 wide at base where its width approximates that of the body; its cuticle unadorned, parenchyma vesicular; posterior one-tenth of tail curved, with terminal invagination receiving ducts of less than 10 unicellular adhesive glands. Oral sucker oval, 0.06 long, 0.04-0.05 wide; ventral sucker 0.06-0.07 in diameter, slightly post-equatorial. Cuticle with many spines 0.01 long, irregularly distributed over entire body except at anterior end. Mouth surrounded by narrow band of spines and by sensory papillae resembling those over body surface and more numerous near anterior end. Prepharynx longer than pharynx; pharynx 0.03-0.04 long, 0.01-0.02 wide; esophagus 0.10-0.11 long but bifurcating well anterior to ventral sucker; ceca reach level of excretory vesicle. Nuclei of genital primordium forms a narrow cord 0.29 long, enlarged at each end. Cephalic glands approximately 20 pairs, mostly lateral to esophagus, with ducts opening anterodorsal to mouth and ventrolaterally in forebody; 2 additional pairs of similar glands in hindbody, with ducts opening just posterolateral to ventral sucker. Body, except at anterior end and around ventral sucker, encased in thick layer of cystogenous material which obscures internal structures. Excretory vesicle small, thin-walled, with subspherical posterior division and smaller anterior chamber receiving separately the primary excretory ducts which extend to prepharyngeal level, expand slightly as they recurve, and terminate just anterior to ventral sucker where each receives anterior and posterior secondary tubules; about 5 ciliated patches in recurrent arm of each primary duct; flame cell formula $2[(3+3+3)+(2+2+2)]$. Develops in 2nd generation redia with long intestine; encysts on various surfaces, preferring exoskeleton of arthropods.

Hosts.—*Goniobasis* spp., *Pleurocera acuta*.

Locality.—Indiana, U.S.A.

Goniobasis sp. in southern Indiana shows a consistently higher incidence of infection with the cercaria of *P. galli* than does *Pleurocera acuta* from the Tippecanoe River but yields far fewer cercariae per snail. It was observed that emergence from both hosts was stimulated when they were placed in the dark after being exposed to light and that when desired, large numbers of cercariae could be obtained by placing snails in the dark after prolonged exposure to light. Then, larvae usually began to emerge within a few minutes and the process was largely completed within 2 hours. When infected snails were placed in the dark for a time and then positioned under the dissecting microscope so that the mantle and gills could be observed through the aperture of the shell, numerous cercariae were

seen in the blood vessels but disappeared from them after exposure to light for a few hours. It was further observed that when mature daughter rediae were removed from the snail and placed in 0.45% NaCl, those kept in the dark released from 5 to 20 times as many larvae as did those in the light. It thus seems that the stimulus of darkness acts directly on the parasites.

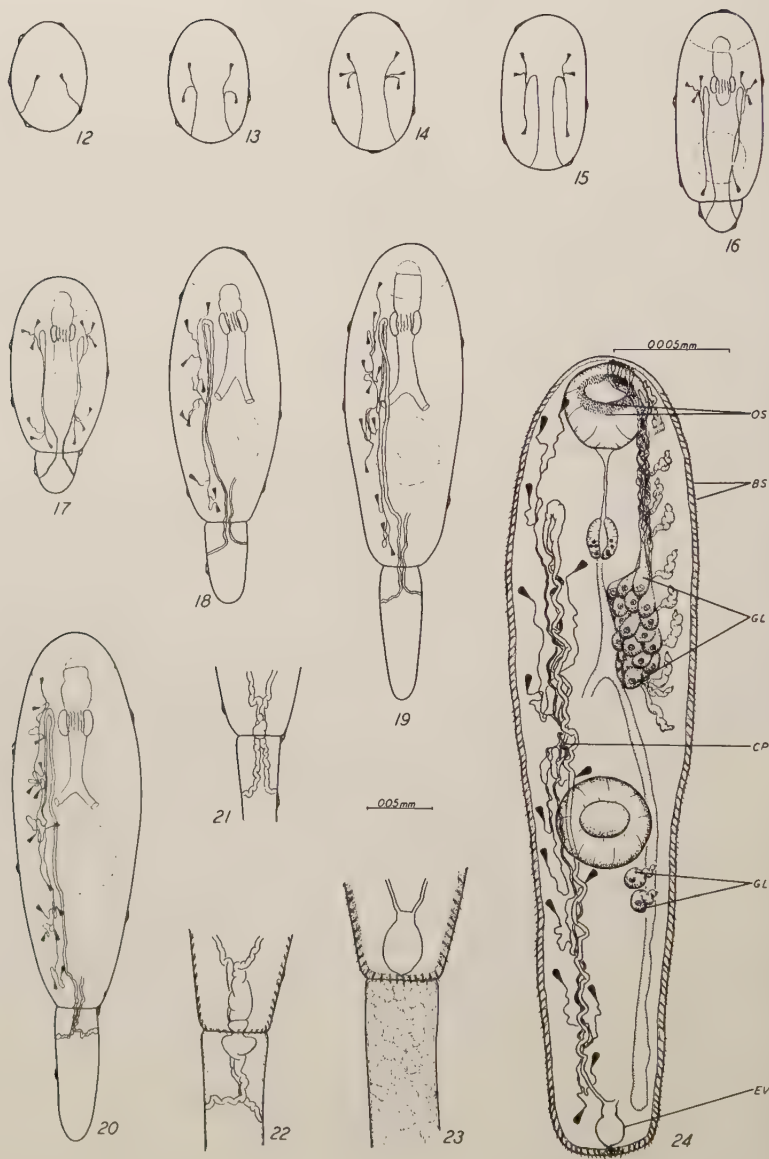
The cercaria of *P. gralli*, like that of *Parorchis acanthus*, is a poor swimmer. In both species, the body flexes strongly and then straightens suddenly in such a manner that the body and tail seem to undulate together. The tail of *P. gralli*, however, is less muscular and has more the appearance of a trailing structure, the tip of which often attaches to objects. Although swimming movements then resemble efforts to pull away, the larva seems able to control attachment by means of the invaginated tail with its associated glands.

If undisturbed, the cercaria may encyst on the bottom of the dish but that process is hastened and more of the larvae form typical cysts if there is movement of the water. Normally, however, contact is made with crayfish, often between its antenna or a process of the exoskeleton and the tail of the cercaria which immediately bends around that structure. The larva then fastens with its ventral sucker and promptly encysts.

The cercaria of *Philophthalmus gralli* possibly is *Cercaria megalura*, a species which, as Cort (1915) pointed out, was erroneously included in the life history of *Megalodiscus temperatus* by Cary (1909). However, the present larva differs in several respects from *C. megalura* as described by Cort. He observed glands (bâtonnet cells) with cytoplasmic rodlets instead of granular cystogenous material that encases emerging cercariae, and he did not observe cuticular spines. Although other differences may be attributed to incompleteness of his observations and preparation of material, the situation with respect to the cystogenous glands and their function needs to be explored further. I searched especially for bâtonnet glands in spontaneously emerging cercariae and embryos of all ages but such glands were not found. Instead, a complex of other glandular structures was observed in some detail and will be described in connection with encystment. On the basis of cystogenous glands alone, the larvae of *P. gralli* and *C. megalura* would seem to be distinct species and the writer is inclined to regard them as such for the time being.

EMBRYOLOGY OF THE CERCARIAL EXCRETORY SYSTEM (Figs. 12-23)

Development of the excretory system in the cercaria is first evident in embryos that have begun to elongate and show on each side a flame cell with a ciliated capillary duct opening posterolaterally (Fig. 12). A 2nd and then a 3rd flame cell appear on each side and the primary pores become more posterior (Figs. 13-14). When the beginning of the tail is barely evident, the primary ducts are recurved



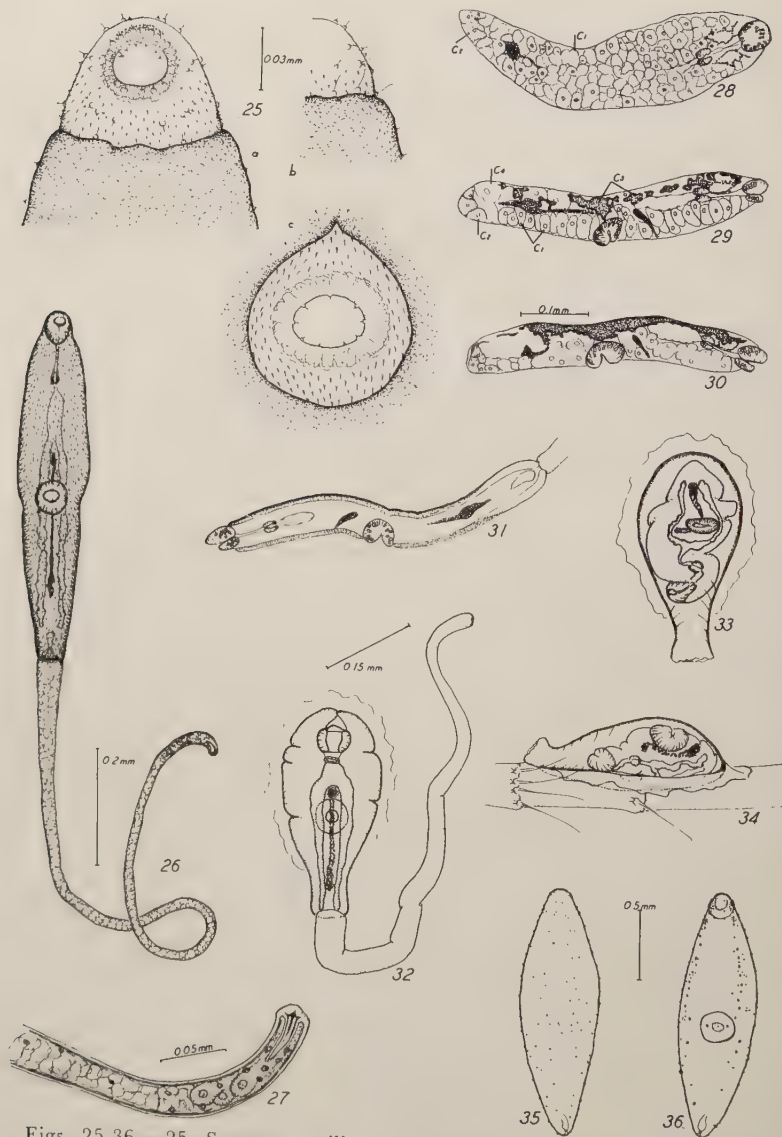
Figs. 12-24.—12-20. Developmental stages of cercarial flame cell pattern (freehand). 21. Excretory vesicle forming (freehand). 22. Same, later. 23. Same, completed, caudal excretory ducts degenerating. 24. Metacercaria showing spines, glands and excretory system (freehand). (Abbreviations as in Figs. 1-4.)

and receive a short anterior capillary with 2 flame cells and a much larger posterior one with a single flame cell (Fig. 15). By the time that the tail bud is well formed and primordia of the suckers, pharynx and esophagus are evident, the 2 anterior flame cells on each side are joined by a third (Fig. 16). Then 2 more flame cells appear near the posterior one on each side (Fig. 17) and the capillaries of three additional ones join each anterior secondary tubule (Fig. 18). The primary pores become relatively farther anterior at the sides of the tail bud and the primary tubules come close together posterior to the ventral sucker. With further growth of the embryo, 3 more flame cells are added to the 6 joining each anterior secondary tubule (Fig. 19) and then 3 to those joining the posterior tubule (Fig. 20). The excretory pattern of the emerging cercaria thus is completed before the posterior ends of the primary tubules fuse to become the excretory vesicle. Excretory structures in the tail then atrophy (Fig. 23) and are not evident in the emerging cercaria.

CYSTOGENOUS GLANDS

Evidently, glands of at least 4 types secrete cystogenous material that was observed at the surface of the fully developed cercaria. In the embryo (Figs. 28-29), 1 type (C_1) occupies the ventral region of the body and consists of large cells with cytoplasm containing numerous eosinophilic granules which are spherical and 1-2 μ in diameter. These glands may correspond to those described by Cort (1915) as containing rod-shaped granules in *C. megalura*. A 2nd type (C_2) consists of a smaller number of distinct cells at the posterior end of the body; they contain minute granules that stain more intensely with eosin. The 3rd type (C_3) is in the dorsal half of the body; they extend almost its entire length and produce granular masses that stain dark with hematoxylin; they have obscure cell boundaries. In the hind body, those masses are interrupted by the 4th type (C_4) which are large and contain globules that do not stain with either hematoxylin or eosin. In the older embryo (Fig. 30), boundaries of cystogenous glands become less distinct and their products condense beneath the cuticle as a dark blue dorsal layer and an eosinophilic ventral one.

Secretions of the 4 types of glands combine in a definite pattern to form the material encasing the emerging cercaria (Fig. 31). The secretions of the C_4 cells cover the posterior end of the body to a thickness of about 10 μ dorsally, somewhat less ventrally, and diminish anteriorly, apparently disappearing at the level of the genital primordium. That material is slightly pink and is intermixed with minute granules from the C_2 glands. The remainder of the cystogenous material surrounding the larva is made up of a layer of large eosinophilic granules from the C_1 glands and, on the dorsal surface only of most of the body, an outer basophilic layer from the C_3 glands. The eosinophilic layer is thicker ventrally and thins out



Figs. 25-36. 25. Sensory papillae and cystogenous material of cercaria; a and b, anterior end; c, ventral sucker (freehand). 26. Cercaria. 27. Tip of cercarial tail (freehand). 28. Embryo cercaria, frontal section showing ventral cystogenous glands. 29. Same, later. 30. Same, sagittal section showing cystogenous glands. 31. Cercaria, showing distribution of cystogenous material on surface of body. 32. Cercaria encysting. 33. Metacercaria cyst. 34. Same, on crayfish antenna. 35-36. Metacercaria, AgNO_3 fixed, showing sensory papillae; dorsal and ventral views respectively. (Abbreviations as in Figs. 1-4.)

posteriorly as the secretion from the C_4 glands increases in thickness, the 2 together maintaining a uniformly thick layer. The basophilic layer becomes very thin posteriorly but extends farther around the body to encompass the posterior end.

ENCYSTMENT AND THE METACERCARIA

(Figs. 24, 32-36)

Before encystment of the cercaria, the acetabulum attaches firmly to a surface which the forebody explores at various angles. Suddenly, the forebody retracts against that surface and a minute amount of a thick substance is exuded through the layer of cystogenous material. Apparently, that exudate and fine wrinkling movements of the body wall cause the dorsal layer of basophilic material to separate from the eosinophilic layer. The basophilic substance then forms the attached part of the cyst and its exposed surface against which the inner layer is molded. Meanwhile, both suckers are strongly retracted into the body of the larva (Fig. 32). Next, its strong contractions evidently force out additional fluids as the eosinophilic layer of granules rapidly soften and the anterior two-thirds of the body tamps that material against the outer cyst wall. Meanwhile, the posterior region of the body remains stationary with the tail still attached, thus determining the peculiar flask shape of the cyst and preventing the deposition of inner cyst material at its narrow end where, as a result, the cyst is thin and fragile. During the first 3 minutes, the inner cyst layer is largely completed and the posterior end of the body becomes active. It then retracts from the neck of the cyst to which the tail may or may not remain attached, and as movements of the larva continue, the suckers evert and the non-staining material over the posterior body region dissolves and swells to fill the neck end of the cyst with a clear semi-solid mass. Although the worm bends and applies the oral sucker repeatedly to the posterior region, release of material from the cephalic glands was not observed. Finally after 10-15 minutes, the larva becomes oriented with the anterior end toward the narrow end of the cyst and thereafter is relatively inactive (Figs. 33-34).

The metacercaria is infective immediately after encystment and undergoes no apparent development during the two weeks or longer that it may remain alive within the cyst. Quick movements are stimulated by a rise in temperature. If that change is sudden, the worm immediately extends its full length in a single movement with the result that the fore body emerges through the neck of the cyst, followed more slowly by the hind body. If the change is more gradual as probably occurs under normal circumstances, the larva emerges less abruptly but begins immediately to migrate away. Numbers of excysted metacercariae thus can be obtained for experimental purposes by pouring warm saline or water over the cysts as reported by Alicata and Ching (1960).

MIGRATION AND LOCALIZATION IN THE DEFINITIVE HOST

Excystment of the metacercariae occurs immediately upon reaching the mouth or crop of the bird and not in the stomach or intestine as in many other digenetic trematodes. Within 3 to 5 hours after ingestion, immature worms may be found not only in the esophagus but also the nasal passages, the orbit and the lobes of the lacrimal gland. Worms were found on the nasal membranes as long as 4 days after infection but thereafter only in the orbit.

The presence of young worms in the nasal passages on the 4th day suggested that they may migrate back and forth from the eye to the nose at will. However, when such worms were transferred from donor chicks directly to the orbit of others, subsequent examination of their nasal membranes never revealed the parasite, thus indicating that once it reaches the orbit, it remains there. The relationships of the nasal passages, nasolacrimal ducts, and their openings suggest that trematodes found on the nasal membranes of chicks had strayed from the direct route to the orbit after leaving the pharynx of the host.

Because nearly all digenetic trematodes, including some philophthalmids, are endoparasites which localize deep within the bodies of vertebrates, the question is raised as to factors responsible for the unusual habitat of *Philophthalmus* species and for their reaching that site. Among those factors that may be mentioned are geotropism, acidity of the proventriculus as a barrier to migration, chemotactic response to nasolacrimal secretions, temperature effects and the high oxygen tension of the orbit.

Although there is an abundance of free oxygen in the orbit, it is difficult to conceive how a gradient could effect migration of worms to that site. Furthermore, when even large numbers of worms were placed in Warburg respirometers and were permitted to remain there for several hours, there was no evidence of oxygen consumption (personal communication, Fisher).

Since metacercariae normally excyst before exposure to the acid secretions of the proventriculus, it was thought that those fluids might repel worms migrating downward, causing them to move in the opposite direction. To test that possibility, use was made of T-tubes filled with 10% fresh egg albumin in 90% Tyrode's balanced salt solution with phenol red as an indicator and made slightly alkaline with sodium carbonate. Proventricular secretions were introduced at one end of the straight side and a narrow beam of light directed through its intersection with the stem in such a manner that convection currents produced a relatively sharp acid-base interface at that point. Excysted metacercariae were then introduced through the stem and their actions followed. It was observed that: (1) Only rapidly migrating worms entered the acid region and then only a distance of about one-eighth inch before stopping and searched about with the forebody. Those unable to find their way out eventually

died. (2) Those moving slowly stopped immediately upon reaching the interface, performed searching motions with the forebody and then withdrew from the interface, moving parallel or at an angle to it. (3) After 1-2 hours, those worms remaining in the alkaline region of the tube continued to move about while those in the acid medium were either apparently dead or lying at the bottom of the tube where they showed weak movements. Although this experiment indicated that the acidity of the proventriculus repels young worms and thus starts them to move up the esophagus, it did not account for their continued migration in that direction to the pharynx and their choice of the orbit by way of the nasolacrimal duct over other sites available through natural passage from the pharynx.

The rapidity with which the young worms can reach the lacrimal glands suggested that its secretions may elicit a chemotactic response on the part of the parasite. To test that possibility, attempts were made to tie off the nasolacrimal duct and thereby block the flow of such secretions, but due to the large size and very thin walls of the duct, the operation was successful in only one bird. Both encysted and free metacercariae were introduced into its proventriculus and crop. Three hours later the worms were found in the esophagus and crop only. The tear secretions were diverted to the outside in another bird in which healing of surgically traumatized ducts blocked them. When it was fed metacercariae and examined several weeks later, no worms were found anywhere. Substitution of excised tear glands for proventricular secretions in the T-tube apparatus showed only that the gland tissue when not intact, apparently is toxic to the parasites.

Although chemotactic response of the parasite to nasolacrimal secretions was not demonstrated *in vitro*, such a role is compatible with failure of Alicata and Ching (1960) and the writer to infect mammals by the oral route. As Bang and Bang (1959) pointed out, the lacrimal ducts of most mammals drain into the anterior portions of the nasal passages and secretions mostly flush the vestibule and spill out the nostrils. Thus they would not all be swallowed as probably occurs in the bird to serve a possible chemotactic role. Also, in such mammals, worms migrating to the eye by way of the nasolacrimal duct would be subject to greater temperature fluctuation than in birds in which the duct opens much farther from the nostrils. When young worms were placed in a petri dish of saline and a small central area warmed, they moved into that area and once there did not leave it. Instead, they concentrated in a small circle near its edge and reacted to the adjacent cool area much as they did to the acid-base interface as described above.

Alicata and Ching (1960) postulated that the occasional human infections may have been acquired by direct ocular infection which they found successful with mammals that could not be infected by the oral route. However, the nasolacrimal ducts in man drain into

the posterior nasal passages as they do in birds, and man may be more susceptible to infection by the oral route than those mammals that have proved to be refractory.

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Life History of the Pigmy Salamander, *Desmognathus wrighti*, in Virginia

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ABSTRACT: Eggs of *Desmognathus wrighti* containing late embryos were found on October 16, 1958, at Whitetop Mountain, Smyth County, Virginia. Transformation in this species occurs prior to hatching. The eggs, hatchlings, and hatching process are described and figured. Recently captured adults of this species engaged in courtship during the fall and spring of 1958-59. The courtship pattern, sex recognition method, and aggressive behavior are described and the spermatophore is described and figured.

INTRODUCTION

During a field study of the ecology of the plethodontid salamanders in the Mount Rogers-Whitetop Mountain area of Virginia, data were obtained concerning several aspects of the life history of *Desmognathus wrighti*. The eggs, hatchlings, and spermatophores were observed in the field and/or the laboratory and are described and figured herein for the first time. The hatching process, courtship, and aggressive behavior were also studied. Specimens discussed in this paper are in the collection of the Museum of Zoology of The University of Michigan.

Travel expenses in the field during the summer of 1958 were defrayed, in part, by a grant from the Horace Rackham School of Graduate Studies of The University of Michigan and funds from an anonymous donor made possible the continuation of the studies during the month of October, 1958. I am indebted to Nelson G. Hairston, Charles F. Walker, and Frederick R. Gehlbach for reading and criticizing the manuscript and to my wife, Della S. Organ, for her assistance in the field and laboratory.

NESTING SITE

Six clusters of *D. wrighti* eggs were discovered on October 16, 1958. All of the clusters were beneath the bank of the headwaters of Big Branch Creek on the north side of Whitetop Mountain, Smyth County, Virginia, at an altitude of 4350 feet. The eggs were at a depth of about 12 inches in a pocket of gravel and mud through which water percolated. The site was saturated and several larvae of *Pseudotriton porphyriticus* and *Eurycea bislineata wilderae* were taken near the egg masses. Excavation of the site was difficult because the bottom of the hole filled with water and the walls collapsed. The final excavation measured three feet on a side by one foot deep.

Each cluster of *D. wrighti* eggs were suspended from the side or the bottom of a small rock with the bulk of the mass projecting into a

small cavity in the mud surrounding the rock. There was only one cluster in each of the small cavities but some of the clusters were within a few inches of one another.

Five egg clusters of *Desmognathus ochrophaeus carolinensis* were also found in this site in "nest cavities" quite similar to those of *D. wrighti*. In addition to the eggs and larvae, 123 *D. wrighti*, 39 *D. o. carolinensis*, 9 *D. f. fuscus*, 4 *E. b. wilderae*, and 3 *P. porphyriticus* adults were collected in the excavation. After removing the eggs, larvae, and adults, the excavation was carefully filled in.

The site was re-examined the following spring. On April 16, 1959, 352 *D. wrighti* were removed from the site. On May 16, 1959, an additional 147 *D. wrighti* were taken in the excavation, but on June 13, 1959, only 26 *D. wrighti* were found. The first snow of the 1958-59 winter season fell on Whitetop Mountain October 25, 1958, shortly after the site was discovered. In early April, 1959, snow was still on the ground in this area. It can be concluded, therefore, that the 649 specimens of *D. wrighti* removed from the nest site in the fall and spring represented a hibernating aggregation.

EGG MASS AND ATTENDING FEMALE

The clusters of *D. wrighti* eggs found on October 16 contained pigmented embryos in late stages of development. The exact number and placement of the individual egg capsules could not be determined, but there were at least two and possibly three concentric transparent capsules. Prior to preservation, the outer capsule of each egg had a diameter of 3.5 mm.

Each mass was a compact cluster of from 3 to 8 eggs (Fig. 1A) suspended by a single attachment stalk. The attachment stalk was merely an extension of the outer capsules of one or two of the central eggs of the mass. Outer capsules of the peripheral eggs of the mass adhered to those of the more central eggs.

An adult was seen with each egg mass but mud-slides, collapsing the walls of the excavation, prevented recovery of the attending adults with their eggs in all but two instances. The two attending adults, taken with their eggs, were females with recently spent ovaries and enlarged convoluted oviducts.

Prior to preservation, the attending females were kept with their eggs in captivity. Each female remained close to her egg mass with the body coiled around the mass and the head either resting upon the eggs or thrust into the center of the mass. Neither female attempted to defend the eggs when disturbed by the observer; both females retreated from the eggs but returned to them shortly after the disturbance ended.

HATCHING PROCESS

Since field work was suspended on October 26, it was not possible to bring all of the egg clusters through to hatching. Four of them,

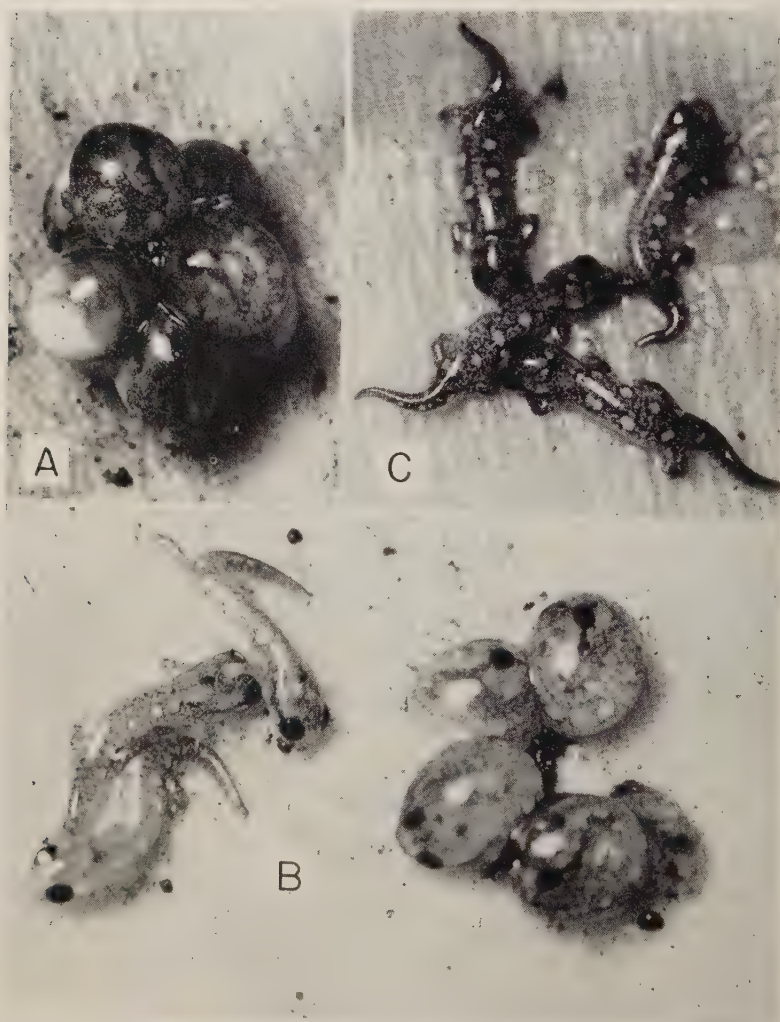


Fig. 1.—Hatching sequence of *Desmognathus wrighti*. A. Eggs containing late embryos; photographed October 16. B. Eggs in process of hatching and hatchlings; photographed October 22. C. Recently hatched young approximately 12 hours after hatching; photographed October 23.

however, hatched either partially or completely in the laboratory (Table I). As the eggs approached a hatching condition, they changed in shape from spheroids (Fig. 1A) to ovoids (Fig. 1B). The encapsulated embryos engaged in vigorous pre-hatching movements, thrusting the head and appendages against the inner capsule (or capsules). They also rotated within the eggs propelling themselves with

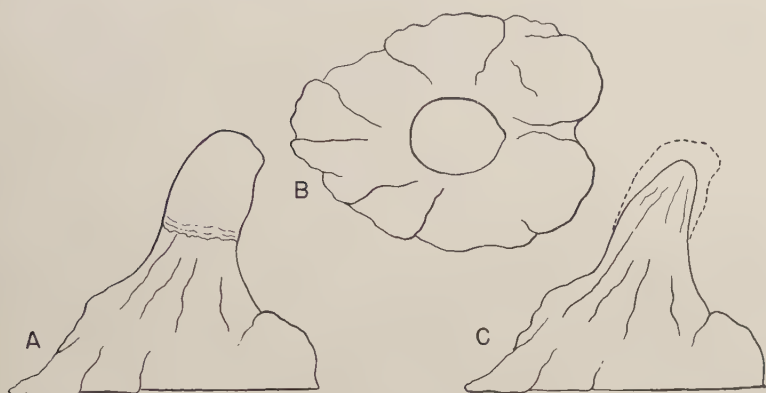


Fig. 2.—Spermatophore of *Desmognathus wrighti*. A. Right lateral view. B. Dorsal view. C. Right lateral view of stalk with position of sperm cap indicated by dotted line.

the aid of the limbs, tail, and flexing of the body. The capsules appeared to weaken in the region of the snout and then rupture. The head and forelimbs of the hatchling were expelled through the rupture points with the escaping egg fluid. The hind limbs and tail were usually freed from the collapsed egg capsules immediately but a few of the young remained in a "semihatched" position for a short period of time. At hatching the young were well coordinated and capable of walking. During the first 24 hours following hatching, they usually

TABLE I.—Clutch number, hatching dates and hatchling size in *Desmognathus wrighti*

Clutch number	Number of eggs	Date hatched	Number hatched	Mean length at hatching in mm	
				Snout-vent	Total
1	3	-----	--	---	-----
2	8	-----	--	---	-----
3	6	Oct. 19-20	6	7.4	10.0
4	5	Oct. 21	2	7.0	10.3
5	7	Oct. 22-23	7	7.9	11.3
6	8	Oct. 24-25	7	8.1	11.2

remained close to the egg capsules but some immediately left the vicinity of the eggs and climbed the glass walls of the finger bowls in which the eggs were kept.

In general embryos within the capsules and recently hatched young were negatively phototropic. The encapsulated embryos rotated until the head was directed away from the light source with the bulk of the body and yolk situated between the eyes and the light. The

hatchlings moved under cover or, in the absence of cover, moved to the less brightly lighted areas of the container.

Many of the hatchlings shed the skin at least once during the first 24 hours after hatching. This same behavior was observed in hatchlings of *Plethodon welleri*.

RECENTLY HATCHED YOUNG

In contrast to other species of *Desmognathus* with known life histories, the hatchlings of *D. wrighti* are not larvae. Gills, present in late embryonic stages as three pairs of long, slender, unbranched, pigmentless structures, are resorbed prior to hatching. The tail of the late embryo is slightly compressed but that of the hatchling is circular in cross section. Caudal fins are lacking in both the late embryos and hatchlings. Mean snout-vent and total lengths of the broods for each clutch are given in Table I.

At hatching the ventral surfaces of the chin, belly, and tail, as well as the undersurfaces of the limbs, are unpigmented. The margin of the lower jaw is pigmented by scattered melanophores. The dorsal pigmentation is determined by the presence or absence of melanophores; no other pigment cells are evident. The unpigmented stripe between the posterior border of the eye and the angle of the jaw, characteristic of this genus, is present in the late embryo and the hatchling. The snout is either unpigmented or lightly pigmented, a condition present in recently transformed individuals of *D. ochrophaeus* (Bishop, 1941).

Well-defined paravertebral spots are present and extend from above the axilla to the proximal two-thirds of the tail (Figs. 1B and 1C). These spots appear yellow in life but are unpigmented. The yellow color results from the underlying yolk mass. The margins of the spots are heavily outlined by concentrations of melanophores. There is another concentration of melanophores in the mid-dorsal line of the trunk, probably representing the anlage of the herring-bone pattern characteristic of the adults of this species. The mid-dorsal line of the distal half of the tail bears an unpigmented stripe.

Three of the five clusters of *D. o. carolinensis* eggs, collected at the same time and in the same site as those of *D. wrighti*, hatched in captivity between October 20 and October 25. Eggs of both species were maintained in the laboratory under the same conditions. Since all of the hatchlings of *D. o. carolinensis* emerged from the eggs as larvae with well-developed gills and caudal fins, it is unlikely that conditions of captivity induced abnormal prehatching transformation in *D. wrighti*. It can be concluded that transformation in *D. wrighti* normally occurs within the egg.

COURTSHIP

Recently captured adults of *D. wrighti* were maintained in 8-inch glass finger bowls throughout the summers of 1957 and 1958, the fall of 1958, and the spring of 1959. Captives were kept on a sub-

strate of moist paper toweling and replaced by fresh salamanders at intervals of two weeks. Spermatophores were found in the containers on the mornings of October 8, April 18, April 20, April 30, May 21, and May 22. Courtship behavior was witnessed during the nights of September 6-7, April 19-20, and May 20-21. Thus, *D. wrighti* has both a fall and a spring courtship period.

The courtship patterns of this and three other species of *Desmognathus* have been described in detail elsewhere (Organ, in press). Sex recognition is accomplished by means of behavioral responses on the part of the individual approached by a courting male. Females either flee from a courting male or remain passive. Males either flee, remain passive, or attack a courting male by biting him. The most frequent response by a male to a courting male is an attack.

The preliminary courtship phases are characterized by the male placing his snout on the dorsum of the female and arching his body upward with the belly and forelimbs raised clear of the ground. The snout and hindlimbs of the male act as anchor points for the arching body. The male violently straightens his body from the arched position and then repeats the arched posture with his snout pressing down on the dorsum of the female. Preliminary stages of courtship are followed by a typical plethodontid tail-straddling walk during which a spermatophore is deposited on the ground by the male (Noble & Brady, 1930; Stebbins, 1949; Organ, 1958, 1960a, 1960b). The tail-straddling walk is usually terminated when the female picks up a sperm cap from a spermatophore with her cloacal lips. The stalk of the spermatophore remains adherent to the ground.

SPERMATOPHORE

In gross appearance the spermatophore of *D. wrighti* (Fig. 2) resembles that of *D. fuscus*, as figured by Bishop (1941), but is smaller. It is 2.5 mm high. There is a colorless, glass-like, jelly stalk and a milky white sperm cap. The stalk is slender and conical with a flaring base of attachment to the substrate. Viewed from above, the base of the stalk is heart-shaped (Fig. 2B). The sperm cap is merely a thin sheath covering the tip of the spike-like stalk. When removed from the stalk, the sperm cap collapses into an amorphous mass.

The surface of the sperm cap is adhesive and clings to objects placed in contact with it. It does not cling to the belly of a courting female, however, when she passes over it. The sperm cap is the only portion of the spermatophore recovered by the female. When recently picked up, it is held between the cloacal lips at the anterior angle of the vent. Eventually, it is withdrawn into the cloaca and ultimately reaches the vicinity of the spermatheca.

The collapsing of the sperm cap into an amorphous mass is typical of the spermatophores of *Desmognathus* in contrast to those of *Plethodon* (Organ 1958, 1960a, 1960b). In the latter genus, the cap retains its shape after being detached from the stalk and does not collapse.

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A New Species of *Echinostelium* from Greece¹

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ABSTRACT: A new species of *Echinostelium*, *E. cribrarioides*, developed in moist chamber culture on poplar bark collected in Greece, is described. It differs from the other three known species in that it forms a well-developed, globose capillitial net. A key to the four known species is provided and the description of the order Echinosteliales is broadened to include this species.

Among a number of Myxomycetes which developed in moist chamber culture on bark from living trees collected in Greece by the author in the summer of 1960, one proved to be an undescribed species of *Echinostelium*. Inasmuch as the characters of this species make it necessary to expand our concept of the order Echinosteliales, this brief article appears to be justifiable.

Echinostelium cribrarioides sp. nov.

Sporangia solitaria vel gregaria, 85-120 μ diam., 0.3-0.5mm. alta, robusta, erecta vel nutantia, ochroleuca, stipitata; stipes erectus, 0.2-0.35mm. altus; peridium fugax, reliquens collare ad apicem stipitis; columella brevis 4-20 μ alta; capillitium ex apice columellae enascens, ramificiens, et reticulum globosum cum paucis terminis liberis formans; sporae globosae, leves cum areolae crassae, pallidae, 9-10 μ diam.; protoplasmodium pallidum.

Sporangia stipitate, scattered or gregarious, globose, 85-120 μ in diameter, 0.3-0.5mm tall, cream colored; stipe hairlike, varying from almost colorless to dark brown, mostly brown below, lighter toward the top, subulate, expanded below and filled with granular material; columella 4-20 μ in height, sharply delimited from the stalk by a conspicuous collar, the remnant of the evanescent peridium; capillitium typically forming a complete, globose net with large meshes, sometimes with one or more free strands extending from it; spore mass cream-colored, supported by the capillitium; spores colorless by transmitted light, 9-10 μ (mostly 9.5 μ) in diameter, the wall smooth, but conspicuously thickened in several more or less evenly distributed areas; plasmodium a colorless protoplasmodium.

Type (GR-14-1960).—Developed in moist chamber culture on bark collected August 6, 1960, from a living *Populus* sp. growing on Mt. Penteli near the monastery of Daou Penteli, north of Athens, Greece. Deposited in the Macbride-Martin Myxomycete Collection, University of Iowa, Iowa City.

This unusual species is described from abundant material which developed on three pieces of bark from a poplar tree near Athens, collected in August 1960, and brought to Iowa City where it was

¹ Part of National Science Foundation project G-6382: An Experimental Approach to the Taxonomy of the Myxomycetes.

placed in a moist chamber. Two or three hundred sporangia developed about a week after the bark was wet. At first glance it was recognized that these sporangia differed from those of either of the two known species of *Echinostelium*, because of their more robust appearance and considerably larger sporangial heads.

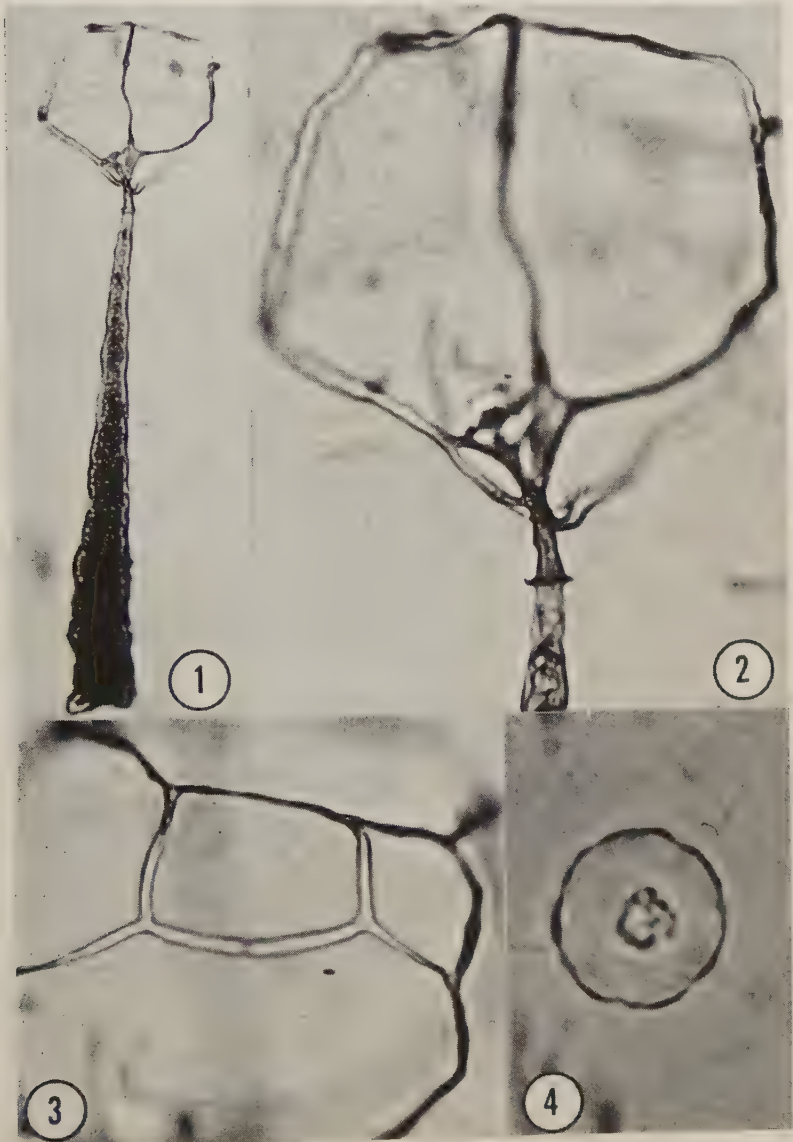
The well-developed capillitial net is the chief characteristic feature of this species (Figs. 1-3). When the sporangia are completely dry, the outer spores of the spore mass are easily dispersed by gently tapping the sporangial stalk with a fine needle. The capillitial net is then exposed often retaining a spore ball inside, giving the fructification the aspect of a *Cribraria*, hence the specific name *cribrarioides* chosen for this species. The peridial collar which remains at the base of the sporangium, and the columella (Fig. 2), from the tip of which the capillitial net originates, leave no doubt as to the nature of the net. It is truly capillitial. The columella and capillitium have a different aspect from that of the stalk. Whereas the stalk is conspicuously granular and in all ways resembles that of *E. minutum* and *E. elachiston* the columella is much less granular, sometimes lacking any granular appearance altogether, and the capillitium is completely homogeneous except possibly at the point of its attachment to the columella.

With transmitted light, the columella and capillitium appear yellow. The capillitial threads are thicker and more robust than those of *E. minutum*, with a diameter of about 2μ .

The spores of *E. cribrarioides* are larger than those of two of the other species, but smaller than those of *E. fragilis*, having an average diameter of 9.5μ and a range of $9-10\mu$. Their structure is characteristic for the genus. The wall possesses a number of thickened areas more or less evenly distributed over its surface. These are particularly conspicuous in the empty spore cases after germination or in spores stained with cotton blue, but can be easily detected in unstained spores under the oil immersion objective (Fig. 4).

Of several attempts to grow this organism in culture only one succeeded. The spores were placed on $\frac{1}{2}$ strength corn meal agar (Difco corn meal agar mixed with equal quantities of 2% plain agar) and a suspension of *Escherichia coli* was poured over them. In about a week several plasmodia had formed. These were colorless protoplasmodia (Alexopoulos, 1960b) much resembling those of *E. minutum* (Alexopoulos, 1960a). The majority of these encysted and could not be induced to develop further. Four, however, proceeded to fruit, each producing a single sporangium. Unfortunately the sporangia in culture were not perfectly developed. The capillitium was rudimentary and obviously aberrant, exhibiting four or five stout main branches but no net. Nevertheless, the nature of the columella and the capillitial branches, the sharp distinction between the stalk and the columella, and the color of the capillitium were all recognizable characters of this species. Attempts to culture the organism again are continuing, but as the material ages the possibility for success becomes smaller.

The discovery of *E. cribrarioides* necessitates a broadening of the description of the order Echinosteliales (Martin 1960) as follows:



Figs. 1-4. *Echinostelium cribrarioides* sp.n.

1. Entire fruiting body after removal of spores $\times 178$.
2. Detail of peridial collar, columella, and origin of capillitium $\times 530$. Detail of upper mesh of capillitial net $\times 530$. Spore $\times 2400$.

Order Echinosteliales

Sporangia globose, stalked, minute. Peridium usually evanescent, rarely persistent. Columella usually present. Capillitium present or absent; when present, either scanty or forming a very open globose net. Spores white, cream-colored, faint pinkish, or golden in mass, colorless, tinged with pink, or golden yellow by transmitted light; spore wall marked with thickened areas, more or less evenly distributed over the surface. Assimilative stage a protoplasmodium.

Family Echinosteliaceae

With the characters of the order.

1. *Echinostelium* deBary; Rost. Versuch. 7. 1873.

With the characters of the family.

Type species, *Echinostelium minutum* deBary.

Capillitium absent

Columella, if present, inconspicuous *E. elachiston*

Columella well-developed *E. fragile*

Capillitium present

Capillitium scanty *E. minutum*

Capillitium a well-developed globose net *E. cribrarioides*

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A Synopsis of *Pinguicula* (Lentibulariaceae) in the Southeastern United States

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ABSTRACT: Six species of *Pinguicula* occurring in the southeastern United States are treated. *P. ionantha* Godfrey is newly described; it is restricted in its distribution to Franklin, Liberty, Gulf and Bay counties, all in the Panhandle of western Florida. A key to the species, descriptions and chromosome counts are included. All species are illustrated.

Wood and Godfrey (1957) in a discussion of the *Pinguiculas* of the southeastern United States treated five species, four of which had previously been known from the area. *P. primuliflora*, there newly described, had been found to occur from southwestern Georgia and western Florida to southern Mississippi. In addition to the morphological features by which it was distinguished, *P. primuliflora* was noted to occur in habitats unusual for *Pinguicula*, namely, in shady areas of spring runs or springy places with *Sphagnum* or *Pallavicinia*, on grassy tussocks, bases of gum trees, and on mill timbers in association with *Orontium* or *Nymphoides*, almost always where there is flowing water. Some specimens were collected in moist, sandy soils in pine-lands but these plants were less well-developed than those from wetter localities. It happens that specimens from the latter, different, type sites comprised two collections from pinelands in Franklin and Liberty counties, Florida, somewhat to the southeast of the more numerous localities for well-developed plants.

During the wet spring of 1960, we visited Franklin and Liberty County localities and discovered well-developed populations of a *Pinguicula* clearly distinguishable from *P. planifolia* and unlike *P. primuliflora* to which species the earlier collections had been assigned. The plants were in shallow standing water of sandy-peaty pineland depressions and broad roadside drainage ditches. Populations of the same plant, again associated with *P. planifolia*, were subsequently located in Gulf and Bay counties, Florida, just to the west. This *Pinguicula* is newly named and described below. The total number of species now known for Florida and the southeastern United States is six.

During the spring seasons of 1960 and 1961 a few plants of each of the six *Pinguiculas* were collected at several localities, the total being about a hundred plants. They were placed in shallow pans of water in the laboratory where they fourished, producing flowers

¹ This investigation was supported (in part by a research grant, RG-6305, to the senior author from the Division of General Medical Sciences, Public Health Service.

continuously for about six weeks. This provided an opportunity to study the plants at leisure, to have illustrations prepared, to describe them in detail, and to make cytological investigations. A key was prepared which may prove helpful in identifying the species, using living material particularly.

Dr. David M. Moore, University of California, Los Angeles, who is presently investigating *Pinguicula* experimentally, has living material of our species. It is presumed that he will study species from various parts of the world and that his employment of newer techniques and criteria will yield a more definitive understanding of species interrelationships and a reinterpretation of the subgenera as reviewed by Barnhart (1915).

Acknowledgments.—The Latin diagnosis for the proposed new species was provided by Dr. Lloyd H. Shinnars, Southern Methodist University, to whom acknowledgment is gratefully made. Illustrations were prepared by Mr. Grady W. Reinert. The generic description below is not meant to be applicable other than to the genus as it occurs in the area under consideration.

GENERIC DESCRIPTION

Plants with a short vertical stem bearing a compact rosette of leaves, the lowermost of which lie flat on the substrate. Leaves entire, those of species whose rosettes are submersed mostly flat, those of terrestrial forms with their sides rolled upward, usually progressively more so toward the tips so that such leaves have a V-shaped outline. Some species, at least, produce buds from the leaves in the latter part of the growing season, these in turn forming new rosettes so that in such forms one often sees, the following season, clusters of rosettes. Flowers produced early in the growing season, each borne singly at the end of an elongate non-bracteate peduncle or scape; each rosette usually producing several flowers but these not all reaching anthesis at once. Glandular hairs, presumably associated with a carnivorous function, occur on the upper leaf surfaces, the scapes, the outer surface of the calyx, to a lesser extent on the outer surface of the corolla tube, and on the ovulary. The glandular secretions impart a greasy character to the surfaces, especially of the leaves. Flowers bisexual, hypogynous, gamopetalous, and 5-merous as to perianth. Calyx two-lipped, the upper lip with three lobes distinct nearly to the base, the lobes closely embracing the upper part of the corolla tube on only one side; the lower lip two-lobed, the lobes not usually incised more than half-way of the calyx and these embrace the lowermost portion of the corolla tube on the same side, the base of the spur extending flush from between the sinus of the lower lip of the calyx. Corolla more or less cylindric-tubular at base, lowermost portion of the tube rather abruptly contracted into a spur; above the tube the corolla flares, bearing five spreading lobes each of which is notched or incised. Corolla attached about midway of the tube and on one side, (the side embraced by the calyx), this part of the tube somewhat inflated, the sexual parts

seated within it at this point (Fig. 1d). From the lower side of the corolla tube just within the throat, projects a hairy palate, in most species extending obliquely outward from the throat, or (in one of ours) included within the throat. Hairs of the palate, of the ridge on the lower side of the corolla tube within and behind the palate, and on the inner side-walls of the tube are more or less characteristic for each species. Androecium comprised of two stamens; filaments thick and stout, arising immediately adjacent to each other on the upper wall of the corolla tube, then arching outward and upward along one side of the ovulary, curving inward again, the anthers nearly meeting and the whole androecium almost outlining a circle through which one side of the ovulary is visible (Fig. 3d). Ovulary subspherical, bearing at its summit two very unequal stigmatic lobes, the lower, larger, nearly orbicular lobe curving downward like a hood and completely or nearly covering the anthers; lower surface of the large lobe of the stigma abundantly clothed with sticky hairs to which the pollen clings. Ovulary 1-locular, with a bulbous free central placenta bearing numerous ovules (Fig. 1d). Fruit a 2-valved capsule. Seeds small, numerous, brown, their surfaces honey-combed.

KEY TO THE SPECIES OF SOUTHEASTERN PINGUICULA

(Constructed especially for living plants)

1. Expanded corolla not, or rarely, exceeding 1.5 cm across; palate not exerted from the throat of the corolla; rosettes rarely exceeding 3 cm broad *P. pumila*
1. Expanded corolla 1.8 cm across or more; palate markedly exerted from the throat of the corolla; rosettes 5 cm broad or more.
 2. Flowers sulphur-yellow or golden-yellow *P. lutea*
 2. Flowers violet to white.
 3. Pubescence on the lowermost portion of the scape consisting of elongated, pointed, multicellular, non-glandular hairs; that of the uppermost portion comprised of 1-celled glandular hairs (transition from one to the other very gradual); expanded portion of the corolla veiny, usually markedly so *P. caerulea*
 3. Pubescence of the scape uniform throughout its length and all glandular; expanded portion of the corolla not at all veiny.
 4. Leaves dull red or reddish-green; lobes of the corolla deeply incised *P. planifolia*
 4. Leaves bright green (although sometimes drying reddish); lobes of the corolla merely notched.
 5. Lobes of the corolla as broad as long or broader; outer 3/4 of the corolla wisteria-violet and with a ring of white above the throat; corolla tube yellow, with reddish-brown veins; trichomes on the inner side walls of the corolla tube yellow *P. primuliflora*
 5. Lobes of the corolla longer than broad; uniformly violet to white (no ring of white above the throat), deeper violet in the throat; corolla tube violet, with darker violet veins; trichomes on the inner side wall of the corolla tube white *P. ionantha*

1. *Pinguicula pumila* Michx., Fl. Bor.-Am. 1:11. 1803. Fig. 1.

Rosettes mostly not exceeding 3-4 cm across. Leaves light-green to olive-green, ovate-oblong, the sides rolling markedly upward from just above the base, more so progressively toward the tip thus forming a V-shaped outline, the tips of the leaves mostly turning downward. Upper leaf surfaces glandular pubescent and with some longer non-glandular hairs on either side of the sunken midrib near the leaf base, these hairs directed across the midrib, crisscrossing each other.



Fig. 1.—*Pinguicula pumila*: a, habitat; b and c, flower, lateral and face view; d, flower, longitudinal section; e, trichomes from palate; f, trichomes from ridge on corolla behind the palate; g, trichomes from inner walls of the corolla tube; h, capsule; i, seed.

Scapes to about 10 cm tall. Lobes of the upper lip of the calyx linear-oblong, blunt, about 3 mm long, those of the lower lip triangular, about 1.5 mm long, olive-green to dull-red. Corollas mostly 1.3-1.5 cm across, the lobes obovate, emarginate, violet to pale violet to white, rarely yellow; corolla tube violet, or yellow, violet mostly only in the deeper violet flowers, faintly to prominently reddish-brown veined; spur dull purplish-brown in the more deeply violet flowers, varying to yellow, veined or not, mostly 3-5 mm long, nearly linear. Palate sulphur-yellow, about 2 mm long, not exserted

from the throat of the corolla tube, clothed with short, stubby, or slightly irregularly knobbed yellow hairs; hairs on the inner ridge of the tube below the palate chrome-yellow to red, with short, stout stalks and knobby tips with very irregular surfaces; hairs on the walls of the tube yellow, more slender, but with very irregularly knobby tips. Filaments white, anthers and pollen very pale yellow or white. Stigma violet to white. Capsule 4-5 mm in diameter. Seed oblong to obpyramidal, mostly ca. 0.3-0.4 mm long, the alveolae mostly with 2-3 cross lines.

Moist, sandy soil, pine flatwoods and savannas. Southeastern North Carolina to the Florida Keys and Bahamas, westward to Louisiana and eastern Texas.

2. *Pinguicula lutea* Walt., Fl. Carol. 63. 1788. Fig. 2.

Rosettes to about 15 cm broad. Leaves yellowish-green, ovate to oblong, the sides rolled upward beginning about 1/3 of the distance from the base, increasingly more so toward the tips until the edges meet, thus the tips have an apparent acuminate tip owing to the curling. Leaves ciliate on the margins near the base, their upper surfaces glandular pubescent, with a few longer non-glandular hairs near the midrib toward the base. Scapes mostly 15-25 cm tall. Lobes of the upper lip of the calyx oblong, broadly rounded at their tips, about 6 mm long, those of the lower lip ovate-triangular, broadly rounded at their tips, about 3 mm long. Corollas mostly 2.5-3.5 cm across, the lobes broader than long, notched or divided to about 1/3 their length, the edges of the lobes smooth to irregular, or occasionally each lobe irregularly 2-3 sub-lobed or toothed. Expanded portion of the corolla sulphur-yellow, not veined, the tube greenish-yellow, usually conspicuously purplish veined on the lower side; spur slender, tapering, 5-10 mm long. Palate yellow, stout, blunt, well exerted from the throat, bearing abundant slender, yellow hairs with slightly enlarged clublike tips; hairs on the inner ridge of the tube, below the palate, with slender stalks and chrome-yellow to orange-red clublike tips having very irregular surfaces; hairs on the walls of the tube yellow, somewhat more slender, with less irregular clublike tips. Filaments white, anthers pale yellow, pollen white. Stigma yellow on the center of the larger lobe, grading to white on the edges. Capsule 7-8 mm in diameter. Seeds mostly oblong, 0.5-0.8 mm long, the alveolae with 3-4 cross lines.

Moist to wet sandy-peaty soils of seepage bogs, pine flatwoods and savannas. Southeastern North Carolina to Lake Okechobee, Florida, westward to eastern Louisiana, on the coastal plain.

3. *Pinguicula caerulea* Walt., Fl. Carol. 63. 1788. Fig. 3.

Rosettes mostly 5-10 cm across. Leaves yellowish-green, ovate-oblong, their sides curling upward from just above the base, progressively more so toward their tips thus forming a V-shaped outline, the tips of the leaves turned downward. Leaves glandular pubescent above and with some long non-glandular hairs near the base on

either side of the sunken midrib, these directed across the midrib, criss-crossing each other. Scapes to about 20 cm tall, densely pubescent, the lower 1/3 portion with long, spreading, pointed, multicellular hairs. Upwards very gradually appear short, 1-celled hairs which produce a bulbous droplet of exudate on their tips. The long hairs very gradually diminish in number up the scape, the short ones become more numerous, the upper part of the scape having only the



Fig. 2.—*Pinguicula lutea*: a, habit; b and c, two flowers, face view; d, flower, lateral view; e, trichomes from the palate; f, trichomes from ridge of corolla tube behind the palate; g, trichomes from the inner walls of the corolla tube; h, capsule; i, seed.



Fig. 3.—*Pinguicula caerulea*: a, habit; b and c, flower, lateral and face view; d, face view of flower with corolla removed; e, trichomes from the palate; f, trichomes from ridge of the corolla behind the palate; g, trichomes from the inner walls of the corolla tube; h, capsule; i, seed.

latter. Lobes of the upper lip of the calyx linear-oblong, about 8 mm long, those of the lower lip lance-triangular or lanceolate, about 5 mm long. Corollas mostly 2.5-3.0 cm across, the lobes cleft from $1/3$ to $1/2$ their length, the subdivisions mostly broadly rounded, sometimes sub-notched or lobed. Expanded portion of the corolla varying from deep violet to pale violet, usually prominently veined, the veins deeper colored than the ground color, sometimes faintly veined.

Corolla tube and spur violet to greenish-yellow, distinctly violet-veined. Spur mostly 5-7 mm long, somewhat tapering. Palate broad and blunt, exserted from the throat, greenish-yellow to cream-colored, abundantly clothed with long, slender, essentially pointed hairs. Hairs on the ridge of the tube within and on the walls of the tube essentially like those of the palate, with barely enlarged tips, or with somewhat branched tips. Filaments white, anthers very pale yellow, pollen pale yellow or white. Larger lobe of the stigma tinted yellow in the center, white nearer the margins. Capsule ca. 1 cm in



Fig. 4.—*Pinguicula planifolia*: a, habit; b and c, flower, lateral view and face view; d, trichomes from inner walls of tube; e, trichomes from ridge of tube behind palate; f, trichomes from palate; g, capsule; h, seed.

diameter. Seeds oblong or obpyramidal, mostly ca. 0.5 mm long, the alveolae with 3-4 cross lines.

Moist to wet sandy and sandy-peaty soils of pine flatwoods and savannas, southeastern North Carolina to Lake Okeechobee, Florida, westward to about the Apalachicola River, Florida, on the outer coastal plain.

4. *Pinguicula planifolia* Chapm., Fl. Southern U.S. ed. 3, 303. 1897. Fig. 4.

Rosettes to about 15 cm across. Leaves oblong, elliptic, or oblanceolate, thin and translucent, flat when fully developed, dull green and slightly to uniformly suffused with a dull purplish-red pigment. Upper leaf surfaces with very short glandular hairs. Scapes relatively slender, to 25 cm high, sparsely glandular pubescent below, more densely so near the summit. Calyx olive-brown or reddish-olive, the lobes of the upper lip oblong, about 4 mm long, those of the lower ovate-triangular, about 1 mm long, all rounded at their tips. Expanded portion of the corolla about 3 cm across, the lobes violet to almost magenta, occasionally nearly white, the throat deeper violet. Corolla lobes incised nearly $1/2$ their length, lanceolate. Corolla tube somewhat veined. Spur oblong, 3-4 mm long, color of the calyx. Palate 4-6 mm long, exserted from the tube, slender, oblong, densely clothed with slender, yellow hairs with smooth to slightly irregularly surfaced clublike tips; hairs of the ridge of the corolla tube within and below the palate with sessile or very short-stalked, druselike hairs, yellow to orange or orange-red in color. Hairs on the wall of the tube within slender, stalked, white, and with smooth to very irregular clublike tips. Filaments pale to deep violet, anthers pale yellow, pollen white. Larger lobe of the stigma deep violet. Capsule ca. 5 mm in diameter. Seed obpyramidal, ca. 6-7 mm long, the alveolae with 2-4 cross lines.

In shallow water, margins of flatwoods ponds, depressions in flatwoods, ditches and shallow drainage canals. Leon, Liberty, Franklin, Gulf, Bay, and Walton counties, Florida, and near Ocean Springs, Mississippi.

5. *Pinguicula primuliflora* Wood and Godfrey, Rhodora 59:219-221. 1957. Fig. 5.

Rosettes to about 15 cm broad. Leaves bright green, more or less oblong, fully developed ones essentially flat, the upper surfaces with short glandular hairs. Scapes rather sparsely glandular pubescent, mostly 8-15 cm tall. Lobes of the upper lip of the calyx 5-6 mm long, broadly ovate-oblong, the lower about 3 mm long, broadly ovate-triangular, all rounded at their tips, dark olive-green, sometimes suffused with a little reddish pigment. Expanded corollas 2.5 - 3.0 cm across, the lobes obovate to sub-orbicular, broader than long, shallowly notched. Open face of the corolla wisteria-violet and with a ring of white just at the base of the lobes and above the

yellow throat, not veined. Corolla tube chrome-yellow, especially within, and prominently reddish-brown veined. Palate chrome-yellow, exserted, cylindrical, 4-5 mm long, densely clothed with clublike yellow hairs. Ridge of the corolla tube behind the palate bearing stout, short-stalked hairs with obovoid or mitten-shaped orange to



Fig. 5.—*Pinguicula primuliflora*: a, habit; b and c, flower, lateral and face view; d, trichomes from palate; e, trichomes from ridge of corolla behind palate; f, trichomes from inner walls of corolla tube; g, capsule; h, seed.

orange-red tips. Walls of the tube with chrome-yellow, slender, clublike hairs. Filaments white, anthers very pale yellow, pollen very pale yellow to white. Larger lobe of the stigma white. Capsule depressed-globose, about 5 mm in diameter. Seeds 0.5-0.7 mm long, obpyramidal to sub cylindric-truncate, the alveolae without cross lines.

In shallow flowing water of springy areas, along small streams, in shallow flowing water of ditches, commonly in dense to open shade. Present records are from the western part of the Florida

Panhandle, Early County, Georgia, and southern Alabama and Mississippi. Earlier records from Franklin and Liberty counties, Florida, were in error.

6. *Pinguicula ionantha* Godfrey, sp. nov. Fig. 6.

Folia laetevirentia spatulata plana usque 4-8 cm longa 2.0-2.5 cm lata. Scapi plerumque 10-25 cm alti parce breviterque glanduloso-pubescentes. Calycis lobi atroolivacei plerumque plus minusve purpurascens; labium superius cum lobis oblongis rotundatis circa 4 mm longis, inferius cum lobis ovato-triangularibus obtusis 3 mm longis. Corolla circa 2 cm lata cum lobis pallide violaceis vel albis obovatis leviter emarginatis 7-9 mm longis 6-7 mm latis; tubo 5 mm longo, cum paucis plus saturate violaceo et venoso; palato conico vel anguste cylindrico 4-6 mm longo exserto; calcar 4-5 mm longo lineari-cylindrico flavo vel olivaceo. Stigmatis lobus inferior violaceus. Capsula depressa-globosa 5 mm diametro. Semina oblongo-cylindrica brunnea 0.6-0.8 mm longa apice truncata vel oblique truncata; alveolae transverse 1-2 lineatae.

Holotype.—Franklin County, Florida: shallow water, depression in flatwoods, 11 miles S of Sumatra; with *P. planifolia*; March 26, 1960, *Godfrey 59362* (deposited in the Gray Herbarium).

Additional specimens.—FLORIDA. *Franklin County*: in shallow water of broad drainage ditch bordering pine flatwoods, 3 miles N. of Carrabelle, March 18, 1960, *Godfrey 59343*; *Liberty County*: boggy margins of drainage ditch through pine flatwoods, 8 miles S of Telogia, March 26, 1960, *Godfrey 59363*; *Gulf County*: shallow water, depressions in flatwoods, 6.5 miles S of Wewahatchka, with *P. planifolia*, March 26, 1960, *Godfrey 59361*; *Bay County*: deep quagmire bog, ca. 11 miles E of Panama City, between Panama City and Wewahatchka, shallow surface water on bog, April 8, 1960, *Godfrey 59390*.

The following two collections were previously assigned to *P. primuliflora* (Wood and Godfrey, 1957). *Franklin County*: common on moist sands of shrub bog-savanna, 15 miles NE of Eastpoint, February 9, 1957, *Kral 4037a*; *Liberty County*: several plants on wet sands along margin of railroad ditch, shrub slash pine bog, 6 miles N of Vilas, Feb. 26, 1956, *Kral 1960 and Godfrey*.

Rosettes to about 15 cm across. Leaves bright green, oblong, rounded at their tips, essentially flat when fully developed, with just the edges rolled upward, the upper surface clothed with short glandular hairs. Scapes mostly 10-15 cm tall, rather sparsely short-glandular pubescent. Upper lip of the calyx with oblong, rounded lobes about 4 mm long, those of the lower ovate-triangular, obtuse, 3 mm long, all dark olive-green and usually suffused with some purplish pigment. Expanded corollas mostly about 2 cm across, the lobes obovate, shallowly notched, longer than broad, pale violet to white. Throat of the corolla and the tube deeper violet than the limb and with darker violet veins. Spur 4-5 mm long, yellow to olive, linear-cylindric. Palate 4-6 mm long, exserted from the throat,

conical or narrowly cylindric, the upper $\frac{2}{3}$ yellow and clothed with yellow, slender clublike hairs some of whose tips turn red as they age; lower $\frac{1}{3}$ of the palate on the upper side violet like the throat and bearing few or no hairs, hairy to the base on the lower side. Ridge



Fig. 6.—*Pinguicula ionantha*: a, habit; b and c, flower, face view, lateral view, longitudinal section; d, pubescence on palate, ridge of tube behind palate, and on inner walls of tube; e, trichomes from palate; f, trichomes from ridge of tube behind palate; g, trichomes from inner wall of corolla tube; h, dehiscing capsule; i, seeds.

of the corolla tube within and below the palate with relatively distant hairs having short, stout stalks and spherical to broadly oblong, orange to orange-red tips. Walls of the tube with relatively few, white, club-like hairs. Filaments pale violet to white, anthers and pollen very pale yellow. Larger lobe of the stigma violet to pale violet. Capsule

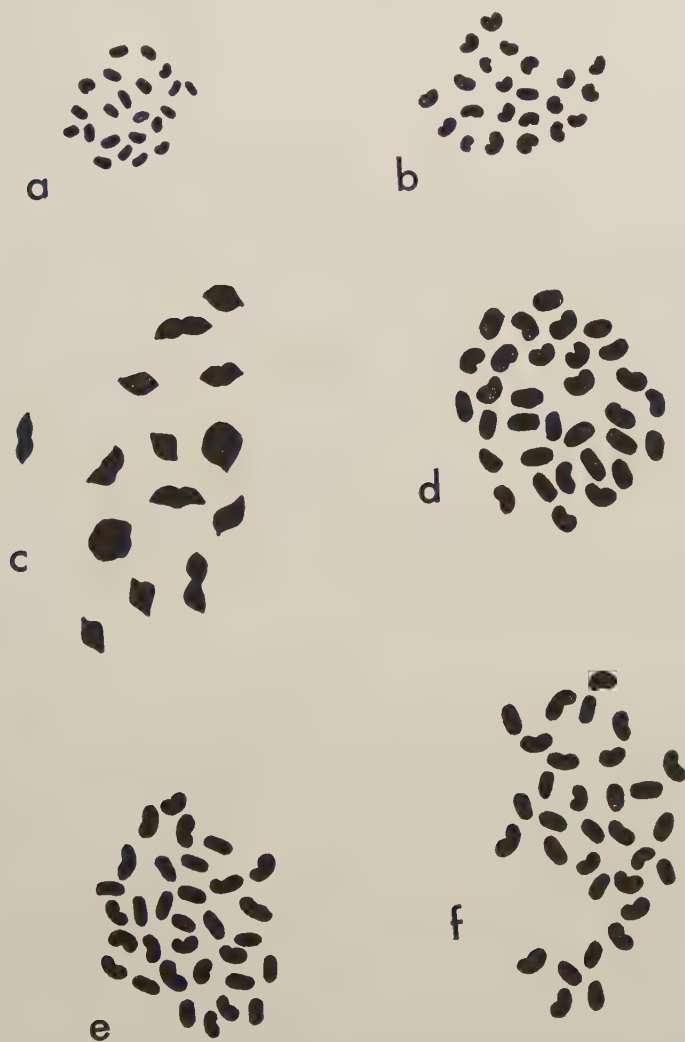


Fig. 7.—Camera lucida drawings of mitotic (except "c" which is meiotic) chromosomes, all approximately X 2800: a, *P. pumila* ($2n=22$); b, *P. ionantha* ($2n=22$); c, *P. caerulea* ($n=16$, twelve bivalents and two quadrivalents); d, *P. planifolia* ($2n=32$); e, *P. primuliflora* ($2n=32$); f, *P. lutea* ($2n=32$).

depressed-globose, about 5 mm in diameter. Seed oblong-cylindric to obpyramidal, the alveolae with 1-2 cross lines.

In flatwoods depressions, ditches, and shallow drainage canals, and bogs, the rosettes mostly submersed (at least when conditions are most favorable); occasional plants, or in occasional places all plants occur in mucky soil bordering such areas. Frequently intermixed with *Pinguicula planifolia*. Liberty, Franklin, Gulf and Bay counties, Florida.

The relatively flat leaves of *Pinguicula ionantha* are very much like those of both *P. planifolia* and *P. primuliflora* in form and contrast with those of the other more terrestrial species the leaves of which curl upward markedly from somewhat above the leaf bases and toward the tips. The leaves of *P. planifolia* are suffused with a dull purplish-red pigment, however, while those of *P. ionantha* are bright green as are those of *P. primuliflora*. The latter two are not known to occur even in the same general area whereas *P. planifolia* and *P. ionantha* commonly occur together. The distinguishing combination of features of *P. ionantha* does not suggest a hybrid origin. This combination of features includes the pattern of coloration of the corolla as well as the actual colors, the characteristic hairs of the tip of the palate and the interior of the corolla tube, the near lack of hairs on the base of the upper surface of the palate, the shape of the corolla lobes, and the cross lines in the alveolae of the seed surfaces. Although *P. ionantha* has some morphological features and habitat "preferences" suggesting affinity with *P. planifolia* and *P. primuliflora*, its chromosome number, $2n = 22$, is the same as that of *P. pumila* whereas the number for all the other four species of our area is $2n = 32$. (See below).

CHROMOSOMES

Chromosome numbers reported previously for the genus were briefly reviewed by Wood and Godfrey (1957). These included the following: $2n=16$ (*P. villosa* L.); $2n=32$ (*P. alpina* L.); $2n=44$ ("*P. caudata*"); $2n=64$ (*P. grandiflora* Lam., *P. vulgaris* L.). The chromosome numbers for the species here treated are listed below together with the vouchers deposited in the herbarium of Florida State University:

- a. *P. pumila*: $2n=22$, Godfrey 60547, 60548, and Stripling 983.
- b. *P. ionantha*: $2n=22$, Godfrey 60552, 60534.
- c. *P. caerulea*: $2n=32$, Godfrey 60542.
- d. *P. planifolia*: $2n=32$, Godfrey 60533, 60551.
- e. *P. primuliflora*: $2n=32$, Godfrey 60532 and Tyson, March 3, 1961.
- f. *P. lutea*: $2n=32$, Godfrey 60535, 60550.

Chromosome counts were made from immature buds. The buds were fixed in a solution of 5 parts absolute alcohol:3 parts chloroform:1 part glacial acetic acid. Counts were made from iron-acetocarmine squashes. See Figure 7 for camera lucida drawings of the chromosomes of each species.

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Morphological Variation Between Local Populations of *Taricha granulosa* in Oregon

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For the past twenty years *T. granulosa* has been considered to represent the stock from which all West-coast forms of *Taricha* arose (Twitty 1942, Riemer 1958). If so, there should be much variation between local populations of this species. The extent of variation has not been detected because specimens from several localities have been combined into a single sample, studies have dealt with a single locality, or only incidentally approach the problem of variation.

This study demonstrates the extent of variation to be expected in common characters within and between areas of a normal part of the range. "Local population" refers to a sample from a single breeding locality. Our method satisfies three requirements: that individuals in each local population be in close contact to assure freedom of gene flow; that distances between collecting sites be great enough to permit morphologic differentiation; that specimens have well developed morphologic characters.

MATERIALS AND METHODS

Collection sites.—During 1952 the senior author collected samples from the following localities: (a) Artificial pond, 300 feet above sea level, on the south slope of Coffin Butte, nine miles north of Corvallis, Benton County. At the time of collecting, June 18, draining operations concentrated the newts in the outlet. The 115 individuals taken probably represented slightly less than one-half the total. Grasses and scattered shrubs surrounded the pond, the bottom of which was black muck resulting from the decay of the dense growth of aquatic plants in and around the edge. (b) On June 21 a collection of 74 specimens was made at Frog Lake, U. S. Highway 26 at Wapinitia Pass, Wasco County, at an elevation of 3800 feet. This small lake is in the typical coniferous forest of the Cascade Mountains. As with the Coffin Butte pond, the bottom of Frog Lake was dark colored as a result of the soil conditions and decayed vegetation; however, the substrate in the lake was much firmer and lightly covered with conifer needles, twigs, and branches. Much of the lake was shaded by numerous trees growing in the shallow water at the edge. (c) During the evening of June 21 a collection of 23 individuals was made at the Crown-Zellerbach mill pond, 400 feet in elevation, two and one-half miles south-east of Molalla, Clackamas County. The area surrounding the pond

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was similar to that around the Coffin Butte pond; however, the Molalla pond had little vegetation and a light colored bottom of tan clay.

It is 46 airline miles from Coffin Butte to Molalla and 41 from Molalla to Frog Lake. Both Coffin Butte and Molalla are in the lower portion of the Willamette River drainage system, while Frog Lake is just to the east of the low crest of the Cascade Range and drains into the Deschutes River via the White River on the east slope of the Cascades. However, Frog Lake, being located at Wapinitia Pass, is only one mile from the Salmon River, which flows down the west slope.

Treatment of the specimens.—Field notes were taken on the color, general appearance, and habitat. Specimens were relaxed in tricaine methanesulfonate (M.S.222), fixed in 10% and preserved in 5% formalin. Immediately after returning to the laboratory measurements were made with a vernier caliper. To avoid the use of juveniles, all specimens with a snout-vent length less than 50 mm were omitted.

Morphologic measurements were made according to standard methods, except for the following: snout-vent length was taken from tip of snout to posterior extent of vent opening, head length from tip of snout to posterior margin of jaw, and nostril-eye distance from posterior margin of nostril to anterior corner of eye.

RESULTS AND DISCUSSION

Coloration.—In life the color of the three populations was noticeably different. Animals from Coffin Butte were dark brown dorsally with yellowish-orange venters and more nearly represented the coloration of *T. granulosa* usually noted. All specimens seen or collected at Molalla were unusually light colored. Dorsal pigmentation was consistently a light milk-chocolate brown. The venters were lemon-yellow with practically no trace of orange. This light hue was in keeping with the light tan color of the pond substrate and surroundings. Individuals at Frog Lake had a dark, blackish-brown dorsal color which blended with the dark substrate. Ventral coloration was a rich reddish-orange, bearing a resemblance to the pigmentation of *T. rivularis*.

Arbitrary classes were established for extent of dorsal color on sides, sharpness of dorsal-ventral color demarcation, and extent of ventral color on the tail. For extent of dorsal color on sides three classes were used: 1 = pigment extended ventrally to about the ventral insertion of the limbs; 2 = pigment came to only slightly below the dorsal insertion of the limbs; 3 = pigment did not reach the level of the limb insertions. Animals from Coffin Butte had 23% class 1, 70% class 2, and 7% class 3; those from Molalla were 39% class 1, 57% class 2, and 4% class 3; the Frog Lake sample was 55% class 1, 45% class 2, and 0% class 3. Dorsal pigmentation was therefore more extensive on individuals of the Frog Lake population.

Three classes were used to denote sharpness of the boundary

between dorsal and ventral pigments: 1 = very sharp demarcation (no melanin grading into ventral pigment), 2 = moderate amount of melanin grading into ventral pigment, 3 = line of demarcation indistinct (considerable melanin grading into ventral pigment). Results for this character were: Coffin Butte 71% class 1, 15% class 2, and 14% class 3; Molalla 26% class 1, 35% class 2, and 39% class 3; Frog Lake 74% class 1, 12% class 2, and 14% class 3. The Molalla population had the greatest degree of melanic suffusion into the ventral color.

For extent of the ventral color on the tail it was necessary to establish five categories: 1 = ventral color from vent entirely to tail tip, 2 = color almost to tip, 3 = color three-quarters of distance from vent to tip, 4 = color one-half the tail length, and 5 = color one-quarter or less. Results for this character were: Coffin Butte 7% class 1, 54% class 2, 37% class 3, 1% class 4, and 1% class 5; Molalla 48% class 1, 43% class 2, 9% class 3, and 0% classes 4 and 5; Frog Lake 12% class 1, 26% class 2, 33% class 3, 29% class 4, and 0% class 5. The Molalla group was distinctive in that ventral pigmentation was more extensive.

Examination of the extent of the melanistic band on the cloacal lips showed that this character was too variable within each local population to be of value in a comparison between populations. Most specimens possessed an incomplete band extending about halfway down the lips, but there was a range from complete absence to complete development.

Riemer (1958) in treating the melanic pigment on the snout of *Taricha* set up nine arbitrary classes. We used only three, but these can be compared reasonably well to figure 15 in Riemer's analysis: 1 = snout pigmented, 2 = snout moderately light, and 3 = snout decidedly light. Coffin Butte specimens were 46% class 1, 51% class 2, and 3% class 3. Molalla individuals were 0% class 1, 65% class 2, and 35% class 3. Frog Lake animals were 51% class 1, 46% class 2, and 3% class 3. These data further bear out the noticeable difference in pigmentation of the Molalla population from that of the other two samples.

Extreme variation exists in pigment distribution and intensity both within and between local populations. Each local population has its own coloration seemingly adjusted to the local conditions. However, overlap is such that one population could be considered preadapted to the conditions of either of the others.

Gular fold.—The gular fold, also highly variable, ranged from very weak to strongly developed, that of the Molalla population being the most pronounced.

Palatine teeth.—The pattern formed by the two rows of palatine teeth had been considered as a rather consistent character for *T. granulosa*. This configuration, closely resembling an inverted V, does vary. Of the specimens examined the range was from the typical inverted V to a pattern resembling an inverted Y. Configurations were ob-

served which fit the patterns for all species of *Taricha* as illustrated by Twitty (1935). Variation might involve the anterior or posterior half of the teeth rows or it might involve the right or left side of the pattern. Among the Coffin Butte sample 11% did not possess the typical pattern, 30% of the Molalla sample were atypical, and 23% of the Frog Lake specimens were variable.

Relation of corneal surface to jaw margin.—For the Californian species of *Taricha*, Twitty (1942) states that in *T. granulosa* the jaw margin extends laterally below the eye, so that when viewed from above, the corneal surface of the eye is not visible in free profile. This is supposedly the result of a smaller eye and broader head than is the case with the other species. In the Oregon populations it was found convenient to set three classes of conditions to compare the samples. These were designated: — for those in which corneal surface did not reach the jaw margin, # for those in which corneal surface coincided with jaw margin, and + for those in which corneal surface extended beyond the jaw margin. It was found that no uniformity existed in the samples examined. Coffin Butte specimens more nearly approached the condition described by Twitty; the results were — 53.2%, # 15.9%, and + 30.9%. Molalla animals were — 4.3%, # 17.4% and + 78.3%. Frog Lake specimens were — 40.5%, # 14.9%, and + 44.6%. Most of Molalla and Frog Lake individuals had corneal surfaces either reaching or extending beyond the jaw margin. With 46.8% of the Coffin Butte specimens having corneal surfaces reaching or extending beyond the jaw margin, this character cannot be considered a reliable criterion for discrimination. In the Molalla sample the condition had reached an extreme (# and + 95.7%), which further set this population apart from the others.

Linear measurements.—The mean snout-vent length for the three populations varied only within 1.53 mm, the Molalla group being the largest with a mean of 72.13 mm and a range of 62 to 81 mm. Coffin Butte was the smallest with a mean of 70.6 mm, but the same range as the Molalla. The Frog Lake group contained the smallest and the largest individuals, showing a range of 59 to 85 mm with a mean of 71.76 mm. With respect to head width the mean varied 1.39 mm. Coffin Butte specimens showed the greatest range, 11.5 to 18.4 mm with a mean of 14.74 mm, and Molalla specimens had noticeably broader heads than the other two, with a mean of 16.13 mm and a range of 13.5 to 18.4 mm. The Frog Lake sample had a mean of 14.76 mm with a range of 13.0 to 16.9 mm. In head length the Molalla animals were the largest, having a mean of 19.65 mm with a range of 17.0 to 22.9 mm, the Frog Lake the smallest, with a mean of 16.18 mm and a range of 13.5 to 19.9 mm, and Coffin Butte the greatest range, 13.5 to 21.9 mm with a mean of 18.08 mm, although not the largest single individual. The mean for this character varied 3.47 mm between the populations.

The largest eye opening was possessed by the Frog Lake population, followed in decreasing order by the Coffin Butte and Molalla

groups. Variation of the means was within 0.66 mm. Means and ranges for this character were Coffin Butte 4.79 mm with 3.8 to 5.5 mm, Molalla 4.3 mm with 3.8 to 4.9 mm, and Frog Lake 4.96 mm with 4.2 to 5.9 mm. The Molalla population, with the smallest eye length and broadest head still had, as previously noted, the greatest percentage of individuals with corneal surface extending beyond the jaw margin. This is explainable by the fact that the eyes of these animals were nearer the periphery of the head as shown by the interorbital distance. Specimens from Molalla had the largest interorbital distance with a mean of 4.86 mm and range of 4.2 to 5.5 mm. Frog Lake was the smallest with a mean of 4.43 mm and range of 3.4 to 5.3 mm. The Coffin Butte sample had the greatest range, 3.6 to 6.3 mm, with a mean of 4.79 mm. The means for this measurement varied within 0.43 mm.

Correlated with the long wide head and small eyes, the Molalla group had the largest nostril-to-eye distance with a range of 3.2 to 4.7 mm and a mean of 3.98 mm. Coffin Butte and Frog Lake populations varied only 0.1 mm in their means. Coffin Butte had a mean of 3.7 mm and a range of 2.8 to 4.5 mm, while the Frog Lake mean was 3.8 mm with a range of 3.0 to 4.5 mm. Variation of means between the three populations was 0.18 mm.

These measurements indicate the decided variation to be expected within and between local populations of *T. granulosa*. It also becomes evident that the robust appearance of the Molalla population observed in the field represents a real difference in body proportions, particularly the massiveness of the head.

Analysis of ratios.—In this study each ratio was determined as a percentage by dividing the smaller measurement by the larger. All statistical calculations are summarized in Table I.

Lack of overlap between the standard errors of head length/snout-vent length indicate that three distinct populations were being examined. The smaller head of the Frog Lake individuals explains the more apparent separation of this group. With respect to head width/head length the Frog Lake population was even more distinct. It again appears to be the result of the smaller head width of these animals. Coffin Butte and Molalla samples, however, were not significantly distinct. It will be noted that the Frog Lake population also spans 88% of the total observed range. Eye length/interorbital distance revealed the distinctness of the three local populations; there was nonoverlap of the standard errors, with an extensive observed range. Small eyes of the Molalla specimens and the smallest interorbital distance of the Frog Lake sample explains their respective low and high extremes.

Eye length/head length showed complete separation of the three local populations. As with the preceding ratios, the Frog Lake population had the greatest range. The extremes of the Molalla and Frog Lake individuals were the result of the respective small eyes and large eyes coupled with the large head length and small head

TABLE I.—Statistical analysis (all measurements are in millimeters)

Sample	No. of Specimens	Range	Mean	Standard Error	Standard Deviation	Variability Coefficient
Head Length to Snout-Vent Length						
Molalla	23	.26-.28	.27	.0020	.01	3.71
Coffin Butte	92	.23-.28	.25	.0010	.01	4.00
Frog Lake	73	.19-.27	.22	.0035	.03	13.63
Head Width to Head Length						
Molalla	23	.75-.88	.82	.0062	.03	3.66
Coffin Butte	92	.75-1.01	.81	.0041	.04	4.94
Frog Lake	73	.78-1.09	.93	.0081	.07	7.53
Eye Length to Interorbital Distance						
Molalla	23	.80-.98	.88	.0104	.05	5.68
Coffin Butte	92	.80-1.27	1.01	.0115	.11	10.89
Frog Lake	73	.88-1.37	1.13	.0128	.11	9.73
Eye Length to Head Length						
Molalla	23	.20-.25	.22	.0020	.01	4.54
Coffin Butte	92	.21-.35	.27	.0031	.03	11.11
Frog Lake	73	.21-.38	.31	.0035	.03	9.67
Eye Length to Nostril-Eye Distance						
Molalla	23	.96-1.32	1.08	.0166	.08	7.41
Coffin Butte	92	.98-1.64	1.31	.0135	.13	9.92
Frog Lake	73	1.09-1.67	1.31	.0128	.11	8.39
Interorbital Distance to Nostril-Eye Distance						
Molalla	23	1.08-1.46	1.23	.0208	.10	8.13
Coffin Butte	92	.98-1.72	1.30	.0135	.13	10.00
Frog Lake	73	.90-1.67	1.17	.0152	.13	11.11

length. Isolation of the Molalla sample as regards eye length/nostril-eye distance was also the effect of the small eyes. No significant difference was observed between the populations when interorbital distance/nostril-eye distance was examined. Range of variation was quite considerable in each population sample.

Ratios of head length/snout-vent length, eye length/interorbital distance, and eye length/head length showed all local populations to be statistically distinct from one another. Head width/head length further served to separate the Frog Lake specimens, while eye length/nostril-eye distance would distinguish the Molalla population. However, examination of standard deviation and range for these characters illustrates the great degree of variation to be expected within and between local populations of *T. granulosa*. The variable tendency of this species is also apparent by comparison of the values of the variability coefficient.

Discussion.—The foregoing data indicate the *T. granulosa* does demonstrate a considerable degree of variation between local popula-

tions. Whether the morphologic entities considered are distribution and intensity of pigment, linear measurements of anatomical parts, relationships of body parts, or degree of development of a selected character does not alter this conclusion. Differences between the three local populations examined are as marked as the differences summarized by Myers (1942) in delineating the subspecies *T. g. twittyi* and *T. g. similans*. This would support Riemer's (1958) conclusion that the species *T. granulosa* has only two subspecies (*T. g. granulosa* and *T. g. mazamae*) that are clearly recognizable. Several of the characters that have been used in the past as morphological criteria for separating the various species of the genus, can no longer be regarded valid. In fact, the extreme variation demonstrated among these three local populations might be interpreted as supportive for Pimentel's (1960) suggestion that the genus *Taricha* consists of only two species (*T. torosa* and *T. rivularis*) with the former being represented by two groups of closely related subspecies. Pimentel suggests that the forms *T. t. torosa* and *T. t. sierrae* belong to one subgroup and *T. g. granulosa* and *T. g. mazamae* to another.

Such variation between local populations of *T. granulosa* undoubtedly is the result of a combination of factors which need further investigation. Geographic mapping of the number and kinds of chromosomal inversions in selected areas of the range of *Taricha* should be enlightening. It is conceivable that the relative inability of these animals to travel any great distances, in a reasonably short time, would reduce gene flow from one local environment to another. The tendency of *Taricha* to return to its place of origin for breeding (Twitty, 1955) would also diminish gene flow between separate local populations. In a widespread form such as this, especially if it is a primitive and plastic stock, these conditions would encourage variation. Yet, through gene transfer from immediately adjacent populations there would be sufficient gene interaction throughout the geographic range to keep the species fundamentally similar in morphologic respects. Under such system the somewhat geographically separated local populations could become adapted to the immediate ecologic conditions, or allowed to express unswamped divergencies.

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Forest History of Martha's Vineyard, Massachusetts

I. Modern and Pre-Colonial Forests

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ABSTRACT: Studies of forest history on the island of Martha's Vineyard, Massachusetts have included three main lines of investigation: a survey of the present vegetation; historical documents relating to colonial land use; and pollen-analytic investigation of postglacial lakes and bogs. Details of the postglacial vegetational and climatic history of the island are the subject of a separate paper. Some evidence from the pollen-stratigraphic studies are included in this paper.

The present vegetation of the Vineyard is in various stages of reforestation following clear cutting, farming, and pasturing. The dominant trees on the island at the present are: Oak, Pine, Beech, Gum, and Hickory. Old-field succession consists of the following stages: Juniper, Pine, Pine-Oak, Oak-Hickory-Beech.

From early historical documents it seems probable that hemlock and white pine were not present in the pre-colonial forests. Other forest trees not mentioned in the historical records of this area, nor found in pollen data include ash, basswood, tulip tree, and chestnut. Although fossil cones of white pine have been found on the Vineyard, pollen studies of the leaf litter associated with the pine cones show no evidence of European occupation at the time the pine cones were deposited.

There is no evidence to show that the early colonists found forests substantially different from those found in the area today. There is some evidence that the trees the colonists found may have been considerably larger with a high canopy.

INTRODUCTION

Although the vegetational history of southern New England has attracted the attention of botanists for many years, there is little agreement upon the nature of the pre-colonial forests. The evidence available, mostly in the form of old travel diaries, indicates that the colonists found forest conditions similar to those of today (Bromley, 1935, Nichols, 1935, Raup, 1937, 1940). Bromley (1935) attributed the open stands and the park-like character of the vegetation of repeated burning by the Indians. Raup (1937) rejected the idea of "... a wholesale conflagration in Massachusetts, Rhode Island, Connecticut, and southern New York as would involve most of the inflammable woods every year, or even every 10 or 20 years (as) inconceivable." Nevertheless, as Lutz (1928) pointed out, fire has been an extremely important factor in determining the composition of the modern forests. There is general agreement, however, that the predominant forest type was a "sprout hardwood" made up of white, red, and black oaks with hickories, tulip trees, and chestnut as an integral part of the association.

There are divergent views on the constitution of the climax, or virgin forests. Fisher (1933), Bromley (1935), and Nichols (1935)

thought that the climax forest for this region was a mixed timber of hemlock and northern hardwoods such as beech, sugar maple, and yellow birch. Their view is opposed by Raup (1937) who considers the "sprout hardwood" as a post-climax type dating from the post-glacial warmth maximum described by Sears (1932). Raup cites the trend toward cooler climates in the past 3000 years as one of the principal reasons for the apparent expansion of the white-pine-hemlock-northern hardwood forest types.

The vegetation of the offshore islands of southeastern New England has received little attention despite a long and richly documented colonial history. Hollick (1894) postulated a land connection between the coastal plain of New Jersey and the offshore islands and Cape Cod on floristic grounds. Fernald (1911) accepted this hypothesis as an explanation of the coastal plain relationships he observed in the floras of Newfoundland and Labrador. Floristic studies of Cape Cod and the offshore islands are restricted to Bicknell's (1919) survey of the vascular plants of Nantucket and a flora of the Elizabeth Islands by Fogg (1930). Despite the larger size and greater relief of the island of Martha's Vineyard, there are no comprehensive floras available. The writings of both Bicknell and Fogg include several references to Martha's Vineyard, in particular to the "more boreal" aspect of the plants of this island.

This discussion will be restricted to a brief survey of the present vegetation of Martha's Vineyard and to those documents and observations on the colonial and precolonial forests which have not received attention elsewhere.

Acknowledgments.—It is a distinct pleasure to recognize the assistance and support of the following individuals: Professor Paul B. Sears of Yale University, whose comments and suggestions in the field and in the laboratory were a great source of encouragement and inspiration; Professors H. J. Lutz and D. M. Smith of the Yale School of Forestry, for many helpful suggestions and the loan of field equipment.

Much of the field work in connection with this study was made possible by a grant-in-aid from the Society of the Sigma Xi and the Research Council of America. I should also like to recognize the encouragement and assistance of my wife, Anne Bowditch Ogden for her enthusiastic and able help in the field and in the laboratory.

Portions of this material were submitted to the Graduate School of Yale University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

LOCATION AND CLIMATE

Martha's Vineyard (Lat. $41^{\circ}25'N.$, Long. $70^{\circ}30'W.$) is an island of approximately 100 square miles. It is the largest of a group of islands south and southwest of Cape Cod, Massachusetts. Physiographically, these islands and Cape Cod form the northernmost outposts of the Atlantic Coastal Plain which dips beneath the sea here and continues eastward as George's Bank. The surfaces of the islands

are of glacial drift and date from the retreat of the Wisconsin ice sheet. Several syntheses of the geological history of this area are available (Shaler, 1886; Woodworth and Wigglesworth, 1934; Flint, 1957).

The moraines which form the northwest coast of Martha's Vineyard have a maximum relief of 300 ft. Their topography is rolling and is in strong contrast to the flat and almost level outwash plain to the east. The soils are rocky, thin, and lack almost every soil component except sand. Successful truck farming is carried on in the "Great Plains," as the outwash plain is locally termed, but near the moraines only pasture farming is practiced because of the rocky soil.

TABLE I.—Climatic Data for Southeastern Coastal New England
(from U.S.D.A. Yearbook, 1941)

Station	January avg.	July avg.	Maximum	Minimum
Nantucket, Mass.	32.6°F.	68.0°F.	92°F.	— 6°F.
Boston, Mass.	26.0	70.0	99	—21
Providence, R. I.	29.5	72.5	100	—17
New Bedford, Mass.	30.7	70.7	102	—12
New Haven, Conn.	29.7	72.6	101	—15

The maritime location of these islands is reflected in the temperature records of this region. (Table I) Although these data are inconclusive, they are representative and indicate that the offshore islands have a distinctly more equable climate than the adjacent mainland.

PRESENT VEGETATION

The distribution of vegetation types found on Martha's Vineyard is shown in Figure 1. The boundaries shown in the diagram have been drawn from aerial photographs and field observations, and are, of course, approximate. For convenience in mapping, some habitat types have been combined: (1) Beach, (2) Salt marsh-Brackish mud flats-Brackish ponds, (3) Fresh water ponds-Swamps-Bogs, (4) Grassland, (5) Scrub-Coppice Forest, (6) Woodland. The vegetation characteristic of these habitats will not be discussed here, but can be found in Ogden (1958).

Bicknell's (1919) flora of Nantucket lists 1108 species of vascular plants, of which 31 per cent are introduced. Of the remaining 69 per cent, over one-half were described as having southern affinities. Fewer than 20 per cent of the native plants were considered to represent northern types. In the Elizabeth Islands, Fogg (1930) described 558 native species and 128 introduced ones. Of the native species, approximately 20 per cent were southern types, and only 9 per cent showed northern affinities.

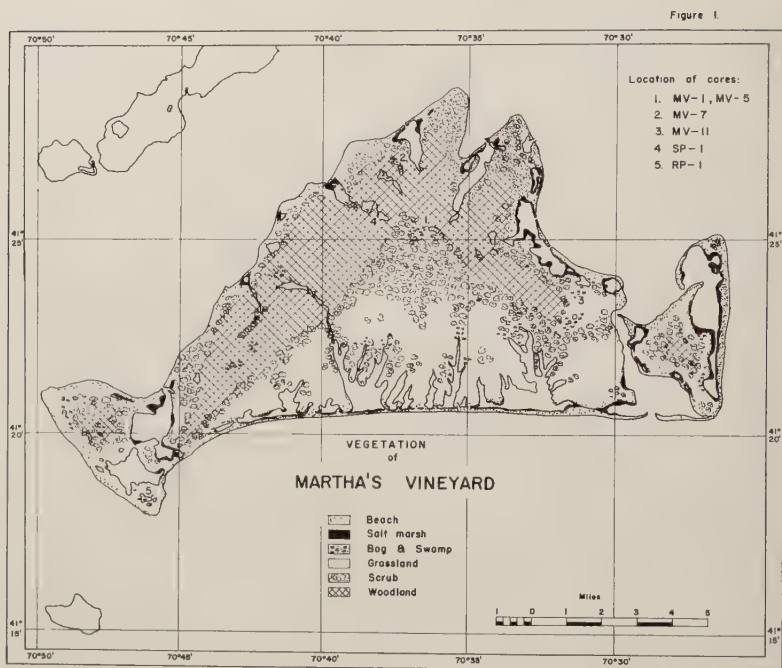


Fig. 1.—Distribution of major vegetational units on Martha's Vineyard. Boundaries determined from aerial photographs and field mapping. Core sites 1-5 indicate locations of samples shown in Figure 3.

Because of the lack of botanical information concerning Martha's Vineyard and the necessity of characterizing the pollen-producing environments there, a list of the plants noted by both Fogg and Bicknell was compiled. Collections and observations were also made in selected localities and added to the list. The number of species whose distribution is primarily south or north of Martha's Vineyard is summarized in Table II. Although no particular importance can be

TABLE II.—Summary of species with northern or southern affiliations

Habitat	No. spp.	No. northern	No. southern	% northern	% southern
Beach	18	6	3	33	17
Salt Marsh	29	6	7	21	24
Bogs, Ponds, Swamps	119	35	18	29	15
Grasslands	85	16	13	19	15
Scrub	60	13	18	22	30
Woodland	64	16	14	25	22

attached to the individual "habitat affiliation" figures (Distribution and range from Fernald, 1950), approximately 27 per cent of the species in this list have southern affiliations, and 33 per cent are primarily of more northern distribution. If this is a valid sample, it indicates that the earlier qualitative observations of Fogg and Bicknell were correct in considering the flora of the Vineyard to be more boreal than that of the other islands. There are far more than 273 species of vascular plants of Martha's Vineyard, but the plants included in this summary are characteristic and the dominant members of the communities in which they occur.

There are a few plants on Martha's Vineyard whose presence marks either a southern or northern limit of distribution. There are no records of new species from Martha's Vineyard, although Bicknell (1919) described a serviceberry, (*Amelanchier nantucketensis*, Bickn.) from Nantucket. This plant is also found on Martha's Vineyard.

MODERN WOODLANDS OF MARTHA'S VINEYARD

None of the woodlands of the Vineyard can be called forests. Some of the better woodlands will probably develop into stratified communities barring further disturbance. These "good woodlands" are restricted to the protected valleys and slopes of the moraine that forms the northwest coast of Martha's Vineyard. The most prominent trees in these stands are white oak, *Quercus alba*; beech, *Fagus grandifolia*; and sassafras, *Sassafras albidum*. These three constitute more than 60 per cent of the tree species on the better sites. Other trees in association with these are: black gum, *Nyssa sylvatica*; black oak, *Quercus velutina*; red oak, *Quercus borealis*; hop hornbeam, *Ostrya virginiana*; pignut hickory, *Carya glabra*; red maple, *Acer rubrum*; American holly, *Ilex opaca*; grey birch, *Betula populifolia*; white birch, *Betula papyrifera* (introduced); black cherry, *Prunus serotina*; dogwood, *Cornus florida*; and aspen, *Populus tremuloides*. Trees characteristic of old-field succession on the island include: pitch pine, *Pinus rigida*; red cedar, *Juniperus virginiana*; and black locust, *Robinia Pseudo-acacia*.

Common understory shrubs include: hobblebush, *Viburnum alnifolium*; highbush blueberry, *Vaccinium corymbosum* and *V. atro-coccum*; witch hazel, *Hamamelis virginiana*; sweet gale, *Myrica gale*; bayberry, *M. pensylvanica*; serviceberry, *Amelanchier canadensis*; Nantucket serviceberry, *A. nantucketensis*; black alder, *Ilex verticillata*; sweet pepperbush, *Clethra alnifolia*; clammy azalea, *Rhododendron viscosum*; dog hobble, *Leucothoe racemosa*; male blueberry, *Lyonia ligustrina*; dangleberry, *Gaylussacia frondosa*; black huckleberry, *G. baccata*; and poison ivy, *Rhus radicans*.

There are a few large trees on the Vineyard and all of the original woodland was cut for firewood or lumber during the early colonial period of the island. Table III lists a few of the largest trees on the island today. This woodland, known as Priester's Woods, is the only area which has developed a definite understory. The greater part of

TABLE III.—Big trees of Priester's Woods, West Tisbury, Massachusetts

Name	DBH (in.)
Black Locust (<i>Robinia pseudo-acacia</i>)	17
Black Cherry (<i>Prunus serotina</i>)	18.5
White Oak (<i>Quercus alba</i>)	35
White Oak (<i>Quercus alba</i>) — (Multiple stem BH)	43.5
Beech (<i>Fagus grandifolia</i>)	49
Beech (<i>Fagus grandifolia</i>)	38
Red Maple (<i>Acer rubrum</i>)	32

the wooded area of Martha's Vineyard is covered with stands of pine (*Pinus rigida*), oak (*Quercus alba*, *Q. Borealis*, and *Q. velutina*), or mixed stands of pine and oak. The growth is characteristically scrubby and extensive tracts of multiple-stemmed oaks between 4 and 6 inches DBH indicate intensive and repeated burning. A few conspicuously older trees in these stands show healed fire scars.

SUCCESION

The general course of plant succession on abandoned crop and pasture land of the Vineyard resembles the Juniper-Oak succession of the New Jersey Piedmont (Bard, 1952) more closely than the grey birch-oak phases described by Lutz (1928) and Raup (1940) for the granitic upland areas of New England. The first tree species to



Fig. 2.—Salt-blast shaping of woodland near shore. Note Juniper (*Juniperus virginiana*)—pitch pine (*Pinus rigida*) succession in foreground.

invade abandoned crop and pasture land on Martha's Vineyard is red cedar, *Juniperus virginiana* (Fig. 2). Unlike the New Jersey Piedmont, however, seedlings of pitch pine (*Pinus rigida*) begin to appear soon after cedars become established. In a few years, the pines form an almost pure stand, with a few seedlings of the oaks which eventually replace the pines. Black oak and red oak are usually more abundant than white oak during the early stages of pine replacement. The black and red oaks form a tangled, multi-stemmed growth within which the white oaks develop. The dense stands of black and red oak force the white oaks into a straight-stemmed habit. It is only after the large, older, black and red oaks begin to die out that more mesic trees, such as sassafras, pignut hickory, beech, and gum appear.

The time required to produce the "pro-forests" is difficult to determine. The pine stands, which form the earliest woodlands on abandoned fields, are usually between 50 and 100 years old when the oaks become prominent. Tree-ring counts of cut cedars indicate that the pines generally become established between 15 and 40 years after the fields are abandoned. In stands where saplings of hickory, beech, and sassafras are found among the predominantly straight-stemmed white oaks, tree-ring counts of the old stag-headed black and red oaks indicate that they are between 125 and 250 years old. Two white oak stumps in Priester's Woods yielded tree-ring counts of 285 and 330 years.

It is impossible to determine the age of the stands accurately by diameter classes. In a woodland not far from Priester's Woods, two black oaks were sampled with an increment borer. One, which had three main trunks averaging 6 inches in diameter was nearly the same age as a nearby single-stemmed tree that was 11.5 inches in diameter.

The Vineyard today, therefore, is somewhat bedraggled in a vegetational sense. The dependence of the early colonists on the forests for timber and fuel is evidenced by the depauperate woodlands. The following discussion deals with the somewhat meagre evidence that is available concerning the precolonial forest and its uses.

PRE-COLONIAL FORESTS OF MARTHA'S VINEYARD

The earliest record of the flora of Martha's Vineyard and the adjacent islands is contained in two journals from the voyages of Bartholomew Gosnold. The account written by Archer (1625) in the form of a diary, is primarily concerned with sailing directions and place descriptions. Brereton's (1602) journal records the plants, animals, and inhabitants of the islands. Although the "colonists" remained only three weeks, Gosnold is generally credited with having made the first settlement in New England which is supported by historical evidence. The exact location of the islands mentioned in the journals is a matter of some dispute. Banks (1911) believes that the first landfall among these islands was on the island that is now called

No Man's Land, although Brereton calls it "Marthaes Vineyard." Of this island, Brereton writes:

The chieft trees of this Island are Beeches and Cedars; the outward parts all overgrown with lowe bushie trees, three or four foot in height, which beareth some kinde of fruits, as appeared by their blossomes (Beach plums, *Prunus maritima*?); Strawberries, red and white, as sweet and much bigger than ours in England, Rasberies, Gooseberies, Hurtleberies, and such; an incredible store of Vines, as well in the woodie part of the Island, where they ran upon every tree, as on the outward parts, that we could not goe for treading upon them: . . .

Of the same island, Archer (1625) writes, ". . . the place is most pleasant . . . we went ashore and found it full of wood, vines, gooseberry bushes, whortleberies (*Vaccinium macrocarpon*?), raspberies, and eglantines (*Rosa rugosa*?)." The Red Whortleberry, (*Vaccinium myrtillus*) of England and Scotland (Hendricks, 1919) does not occur in North America. The Large, or American Cranberry (*V. macrocarpon*) is very common on the offshore islands and resembles *V. myrtillus* sufficiently to be mistaken for it. The American Cranberry occurs on coarse sandy soils near the coast where tree growth is sparse, rather than in open bogs, swamps, and wet shores (Fernald, 1950). Although *Rosa rugosa*, the beach rose is described (Fernald, 1950) as being introduced and naturalized from Asia, there is no other native plant with which the colonists could have confused the well-known eglantine (Hendricks, 1919).

Anyone familiar with the shore regions of these islands will realize that this is an accurate description of what may be seen today on the coasts of most of these islands. Large numbers of beach plums (*Prunus maritima*), beach rose (*Rosa rugosa*), and cranberries (*Vaccinium macrocarpon*) are near the beach, and great quantities of wild grape (*Vitis Labrusca*) cover many of the trees and most of the ground adjacent to the beaches.

Although this island may have been Martha's Vineyard, there are some discrepancies in the chronicles which make this interpretation unlikely. Brereton speaks of an island "Foure English miles in compasse. . . ." Archer mentions that the island is "five miles in circuit." This part of the description fits No Man's Land very well. The chronicler (Brereton) goes on, however, to describe ". . . many springs of excellent sweet water, and a great standing lake of fresh water, neere the sea side, an English mile in compasse. . . ." This description does not resemble anything now found on No Man's Land. The description does fit the present island of Cuttyhunk, the most seaward of the Elizabeth Islands. Unfortunately, the next few paragraphs in Brereton's account make Cuttyhunk an impossibility, for he writes, ". . . from hence we went to another island, to the North-west of this, and within a league or two of the maine, which we found to be greater than before we imagined, being 16 English miles at the least in compasse; . . ."

There are no islands to the northwest of Cuttyhunk, and of the islands to the northeast (the Elizabeth Islands, Naushon, Pasque, Nashawena), none are "16 English miles in compasse . . ." If the first island was No Man's Land, however, then this island would have to be the present Martha's Vineyard. A difficulty with this interpretation is the fact that the Vineyard is nearer to sixty miles in "compasse" than sixteen. Banks (1911) believes that the second island was the present Martha's Vineyard. Howe (1943) on the other hand, believes that the first island described by Brereton and Archer was Martha's Vineyard and was so named by them. Archer's account, however, makes it more probable that the first island was No Man's Land, for he writes, ". . . we set sail (from the first island), and doubled the cape of another island next unto it, which we called Dover Cliff . . ." These cliffs could only be the Gay Head cliffs of Martha's Vineyard. Both authors refer to the red and gray clays that can be found there.

If the ship's company actually did fortify an island in a lake on Cuttyhunk Island (as both Howe, 1943 and Banks, 1911 agree), then the concluding paragraph from Archer's account confirms the identification of the islands. Archer writes, ". . . we set sail, doubling the rocks of Elizabeth's Island (Cuttyhunk and Sow and Pigs Reef), and passing by Dover Cliff (Gay Head Cliff on Martha's Vineyard), came to anchor at Martha's Vineyard (No Man's Land) . . . (The following day) we set sail and bore for England . . ."

Both Banks (1911) and Howe (1943) point out that the place descriptions and locations could have been deliberately confounded to prevent rival navigators from finding the area and capitalizing on the published descriptions. If the "Dover Cliff" of Archer's account is the present Gay Head Cliff of Martha's Vineyard, the following quotation from Brereton refers to the vegetation of Martha's Vineyard (modern):

This island (the second island) is full of high timbered Oaks, their leaves thrice so broad as ours; Cedars straight and tall; Beech. Elme. Hollie, Walnut trees in abundance, the fruit as bigge as ourse, as appeared by those we found under the trees, which had lien all the yeere ungathered; Hazlenut trees, Cherry trees, the leafe, barke, and bignesse not differing from ours in England, but the stalke beareth the blossomes or fruit at the end thereof like a cluster of Grapes, forty or fifty in a bunch; Sassafras trees great plentie all the Island over, a tree of high price and profit; also divers other fruit trees, some of them with strange barks, of an Orange colour, in feeling soft and smoothe like Velvet; in the thickest part of these woods, you may see a furlong or more round about. . . . Also, in every Island, and almost every part of every Island, are great store of Ground nuts, fortie together on a string, some of them as bigge as hennes egges; they grow not two inches under ground; the which nuts we found to be as good as Potatoes.

In a subsequent portion of the chronicle, Brereton also mentions

"Cypres trees, and Cotton Trees . . .", which are probably *Populus* sp. and *Juniperus* sp., respectively. The "Cedars, tall and straight . . ." are probably the coast White cedar, *Chamaecyparis thyoides*. Extensive swamps containing large specimens of this tree are known from Cape Cod and other parts of New England (Deevey, 1948; Nichols, 1935). The walnut trees of the chronicle are undoubtedly hickories, as walnut was a general term for both walnut and hickory in early writings. The cherry trees can only be the Wild Black Cherry, *Prunus serotina*, which is one of the most common roadside trees on Martha's Vineyard today. The "fruit trees" with velvety-orange bark are much more difficult to recognize. A common open-field plant, which does attain the size of a small tree, is the staghorn sumac, *Rhus typhina*. The only other tree which comes to mind is the hophornbeam, *Carpinus caroliniana*, however, the bark is hardly velvety and the trunk a very dubious orange color.

On the basis of the description of the ground nuts by Brereton, ". . . in every Island, and almost every part of every Island . . . as bigge as hennes egges . . ." it seems likely that the groundnut, or wild bean, *Apios tuberosa* is indicated. Hendrick (1919) remarks that these groundnuts had a flavor not unlike potato.

Two comments from Brereton's chronicle give some clue to the structure of the forest, ". . . the woods of this island were full of high timbered Oaks . . . (and) in the thickest part of these woods, you may see a furlong or more round about . . ." In view of the detail with which Brereton recorded the trees which he saw, there is little reason to doubt that he did see "high timbered oaks . . .", a situation not found in any part of the island of Martha's Vineyard or any of the other islands today. Because of dense underbrush and multi-stemmed growth of the modern woodlands, it is difficult to see 50 yards in the best of the woodlands, much less the 200 or more yards indicated in the journal. These two statements would seem to indicate that some parts, if not most of the island was covered with a high canopy forest, a condition not approximated by any of the modern woodlands of these islands.

Another indication of sizeable trees in the early Vineyard forests is the record of a whaling ship 135 feet long, of 65 tons burden, that was constructed of Vineyard timber prior to 1850 (J. C. Allen, personal communication). Although the keel was spliced, there are no oaks on the Vineyard today which approach the dimensions required for this construction. All of the native woodlands were eventually cut, and most of the cleared land was used for pasturing and farming (Banks, 1911). It is impossible to walk anywhere on the island today without seeing stone walls criss-crossing through the woods.

The colonists were not blind to the effects of clear-cutting and the potential denuding of the landscape. Many farmers maintained woodlots for household firewood, fence posts, and gate timbers. There is at least one well-authenticated instance in which two families cut

all of their stove and winter firewood from a 40 acre plot for well over 100 years (J. C. Allen, personal communication). Colonial axemen can be rated by the character of the stump sprout woodland which they left: a good axeman left a single "header" from which a single sprout would develop; a careless, or unskilled axeman would leave a "frazzled head" from which two or more sprouts would develop. This is evident in woodlands now found on croplands abandoned 75 or 100 years ago. Stem measurements and three-ring counts indicate that "single sprouts" may be twice the diameter of multiple sprout stems, even if they are of the same age.

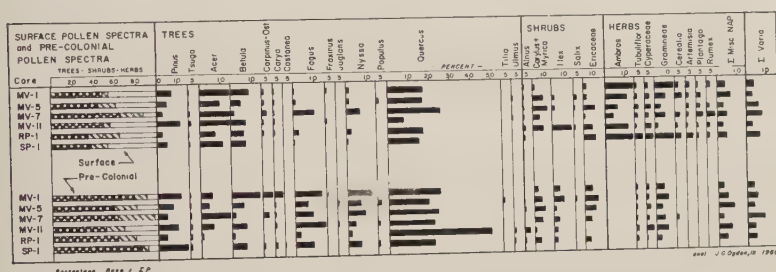


Fig. 3.—Pollen spectra from selected cores on Martha's Vineyard. The sample locations are shown in Figure 1. The upper six samples represent the modern vegetation in the vicinity of the sample site, and the lower six samples represent the pre-colonial vegetation (based on the lack of clearance/agriculture pollen indicators in the Herb columns on the right of the diagram). The sum of tree pollen is shown with double hatching in the block diagram at the left; the sum of herbaceous pollen is shown with single hatching; and the sum of herbaceous pollen (exclusive of the pollen of aquatic plants) is shown clear. The bar graphs represent the per cent of all pollen of each type at that level. A per cent scale is shown at the top of each histogram to facilitate comparison.

EVIDENCE FROM POLLEN ANALYSIS

A comparison of pollen spectra from surface samples of modern lakes and bogs on Martha's Vineyard with pollen spectra from pre-colonial times is shown in Fig. 3. The location of the sampling sites is shown in Fig. 1. The laboratory methods used to prepare the samples have been described elsewhere (Ogden, 1959). The principal criterion for the selection of the latest pre-colonial pollen sample was the absence of any European weed pollen (*Plantago*, *Rumex*, *Artemisia* cfr. *maritima*).

There is a higher representation of tree species in the pre-colonial samples than in the surface (modern) samples, due primarily to the abundance of Ambrosia type and Grass pollen in the surface samples (Fig. 3). The most significant results of this approach can be seen in a comparison of the trees contributing to the pollen samples in each of the two sample series. There is very little hemlock, hickory,

ash, walnut, cottonwood, basswood, or elm pollen in either of the sample series. There is no chestnut pollen in either sample series. Beech and gum appear to exhibit a reciprocal relationship with the pollen of maple. Although species identification of maple from pollen alone is not very reliable, the pollen types identified, as well as the present distribution of maple of the Vineyard, indicates that these are probably the pollen grains of red maple (*Acer rubrum*). The decrease in beech and gum in the modern forests is apparently real, and reflects a former forest composition which contained many more specimens of these trees.

These data indicate that the pre-colonial forests of Martha's Vineyard did not contain any different trees than are now found on the island, but rather, that the present "better woodlands," now found only in restricted sites in a small part of the island, were once more widespread. Brereton's chronicle mentions, "... Walnut trees (Hickory) in abundance ..." In the present Vineyard woodlands, hickory is not common, and is found only in the more mature woodlands within which a definite understory has developed. The cutting and burning practices of the early colonists could be expected to eliminate those tree species which could not readily form stump sprouts or those species which were especially prized for their wood. Species which can form stump sprouts readily, such as oak, could be expected to survive. Oak is also able to withstand the decrease in soil moisture that accompanies wholesale clearing better than the more mesic trees such as beech and gum.

Another factor influencing the process of revegetation after abandonment of fields on the Vineyard is salt-blast. Once the fields are open to the sweep and force of winter storms, the toxic effects of wind-blown salt (Boyce, 1954) undoubtedly limit reforestation, especially in the coastal areas (Fig. 2).

The picture of the colonial and pre-colonial forests which emerges from these observations is still incomplete. Nevertheless, the following generalizations seem justified on the basis of the evidence described in the preceding paragraphs:

1. The scrubby nature of the modern woodlands can be attributed to the formation of stump sprouts in areas cut over by colonial axemen. Destruction of seed sources and salt-blast have limited reforestation.
2. At least some portions, if not all, of the Vineyard were covered with a high canopied mature forest when the first colonists arrived.
3. Hickories were probably more abundant in the pre-colonial forests than at present.
4. Hemlock, chestnut, ash, walnut, basswood, and elm were either absent from or a very minor constituent of the pre-colonial forests.

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The Red Eye Pigment Content of the *Drosophila affinis* Subgroup Species

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ABSTRACT: The red eye pigments of *Drosophila algonquin*, *D. azteca*, *D. melanogaster*, *D. narragansett*, *D. pseudoobscura*, and *D. tolteca* were analyzed. The determinations confirm the close relationship of the *D. obscura* group species as compared to *D. melanogaster*. *D. azteca* and *D. tolteca* appear to be very closely related; whereas, *D. pseudoobscura* was shown to possess an appreciably lower amount of red eye pigment than the *D. affinis* subgroup species.

A definite correlation was found to exist between the size of the eye and the red pigment contained therein, but the relationship varied from species to species. Instances of significantly great variability between strains of single species were found in *D. affinis* and *D. melanogaster*.

The fact that the color of the eye of wild-type *Drosophila* is due to two pigments, red and brown, resulting from two different biosynthetic pathways has been established by several experimental techniques. The identification of the sequence involved in red pigment formation has been particularly difficult to elucidate and only in recent years has the mystery begun to be unveiled. A number of pteridines which are ostensive precursors of red pigment have been identified (Hadorn and Mitchell, 1951; Forrest and Mitchell, 1954, 1955; Forrest, Hatfield, and Van Baalen, 1959). Visconti, Hadorn, and Karrer (1957) isolated three red pigments from the eye of *Drosophila melanogaster* by paper chromatography. These pigments, apparently closely related to their pteridine precursors, have been named drosopterin, isodrosopterin, and neodrosopterin, and they may be extracted simultaneously and measured quantitatively.

Members of the *D. affinis* subgroup are widely distributed geographically (Miller, 1958) and are very similar and closely related as evidenced by the mating experiments of Ensign (1960), Miller (1950a, 1950b), and Ensign and Miller (1957). Sulerud (1958) has indicated that the sex combs and tarsi of these species may be promising criteria for identification purposes and that overlapping of characteristics does occur although it is limited.

The purpose of this study is to determine whether the red pigment content of the *D. affinis* subgroup might be used as an aid in establishing the relationships of the individual members which are considered.

¹ This paper is taken from a master's thesis presented to the University of Nebraska and is contribution number 333 of the Zoology Department of the University of Nebraska.

Acknowledgments.—I am deeply indebted to Dr. Dwight D. Miller who served as my advisor during the tenure of this research and who supplied many stimulating comments and suggestions. Gratitude is also extended to the Zoology and Physiology Departments of the University of Nebraska who made their research facilities available to the author.

EXPERIMENTAL METHODS

Species and strains of *Drosophila* used for the major portion of this study were: *D. affinis*, Missouri (Halls) and North Carolina (Raleigh); *D. algonquin*, Nebraska (Humboldt) and Minnesota (Halstad); *D. azteca*, Mexico (Durango) and California (Mather); *D. melanogaster*, Nebraska (Niobrara State Park) and Texas (Waxahachie); *D. narragansett*, New York (Lebanon); *D. pseudoobscura*, British Columbia (Kelowna) and Mexico (Hidalgo); and *D. tolteca*, Mexico (Chapulucán) and Bolivia (Coroico).

The inclusion of the strains of *D. melanogaster* and *D. pseudoobscura* was stimulated by the earlier work of Nolte (1958) in which he demonstrated a decisive difference between the pigment contents of the eyes of these two species. All the strains utilized were established from a single wild female except the Minnesota strain of *D. algonquin* which is a mixed strain. Because it was thought that any intraspecific variations might be revealed by using strains established from flies far removed from each other, each species, except for *D. narragansett*, was represented by widely separated strains from two localities.

Ephrussi and Herold (1944) showed that the amount of red pigment decreases with an increase in temperature. The total amount of pigment is also dependent on the size of the eye and thus presumably is related to the size of the fly. Thus it was desirable to acquire flies of optimum adult size for experimental analysis; consequently, the flies were grown on freshly prepared cornmeal medium which was supplemented with an abundance of live yeast and the temperature was controlled at $18 \pm 2^\circ \text{C}$. To avoid overcrowding of the larvae and adult flies, eggs were collected and the number of flies per bottle of culture medium was limited to less than 120.

In regard to the adult flies, Ephrussi and Herold (1944) have shown that there is a change in red pigment content of the eye with increase in age; however, the increase of pigmentation does reach a point of stability after several days. The period of time before the red pigment content became stable was found to be slightly longer than the five-day period that Ephrussi and Herold indicated; consequently, the adult flies were aged for a ten-day period after which no increase in red pigment deposition was evident.

The extraction procedure utilized was essentially that of Ephrussi and Herold (1944). The solvent which has been named AEA was prepared by adding 1.0 ml of concentrated HCl to 1000 ml of 30% ethyl alcohol. A large volume of AEA was made up and used throughout the experimental work. The pH of the solvent was checked period-

ically with a Macbeth Continuous Operating pH Meter, and it was found that the pH did not deviate from 2.0 during the time that the AEA was being used; therefore, the solvent was not a variable.

The heads of the flies were removed and diameter of the head was recorded by measuring across the eyes with a 2 mm micrometer. The heads were then partially split between the eyes with the edge of a razor blade and extracted in the dark at $18 \pm 2^\circ \text{C}$ with AEA for $2\frac{1}{2}$ to 3 days. The size of each sample was 20 heads per 4.0 ml of AEA.

Following extraction the light absorption of the solution containing the red pigment was determined photometrically through the 400-540 $m\mu$ light spectrum with a Beckman D. U. Spectrophotometer and 485 $m\mu$ was found to be the maximum. The results of the light absorption measurements of the red pigment extracts will be given in terms of extinction, $\log I_0/I$.

The red pigment solution behaves as a redox system, being light brown in the oxidized state and colorless in the reduced state. However, Ephrussi and Herold have clearly shown that the extracted pigment is in the state of maximum oxidation; therefore, no precaution was necessary to control the oxidation state of the extracts.

RESULTS AND DISCUSSION

Following the methods outlined, flies were raised under controlled conditions in an attempt to obtain adult flies of optimum and uniform size. By measuring the diameter of the decapitated heads the uniformity of head size was under close observation, and it was readily observed that there was a striking variation of head size between species (Tables I and II). This was true although all species are members of the *D. obscura* group except *D. melanogaster*; and, moreover, *D. affinis*, *D. algonquin*, *D. azteca*, *D. narragansett*, and *D. tolteca* are members of the *D. affinis* subgroup. *D. algonquin* and *D. pseudoobscura* were found to have comparatively large heads; whereas, *D. tolteca* and *D. azteca* had small heads, and the other species were intermediate in size.

The diameter of heads of females was found to be greater than that of males, and this was also true of body structure in general. The means of head diameter of each sex of the laboratory strains are given in Tables I and II, are accompanied by the standard error and range of individual samples to facilitate visualization of the variability.

Variability was found to be relatively large between individual flies. This might be explained by differences in larvae feeding conditions; however, the adult flies emerged from pupae within a two day span. Therefore, differences in feeding conditions with which the larvae were confronted should have been slight. In spite of the individual variance, the means of the head diameters of the samples within a strain were found to exhibit less variability, and in most instances the variability was less than 3%

Qualitatively the red eye pigment extract was the same for all the laboratory strains that were tested. The curve formed by plotting extinction against light wavelength was similar to that which has been described by Nolte (1952) and others. The rather broad peak which is formed in this manner is the result of the mixture of at least three different drosopterins with slightly varied absorption maxima. The values given in Tables I and II are the extinction values at 485 m μ for the extract of twenty heads in 4 ml of AEA.

In regard to the red eye pigment content of the laboratory strains that were tested, a similar variance was found to exist in comparison

TABLE I.—The means for head diameter in mm and extinction of the red pigment extract are given for the males of the laboratory strains that were tested; the number of samples (n) is indicated

Laboratory strains	n	Head diameter	Extinction at 485 m μ
<i>D. affinis</i>			
Missouri	4	0.817 $\pm$ 0.005 (0.805—0.827)	0.471 $\pm$ 0.008 (0.453—0.491)
North Carolina	4	0.806 $\pm$ 0.007 (0.793—0.820)	0.381 $\pm$ 0.009 (0.364—0.403)
<i>D. algonquin</i>			
Nebraska	4	0.883 $\pm$ 0.004 (0.876—0.895)	0.452 $\pm$ 0.005 (0.438—0.463)
Minnesota	4	0.847 $\pm$ 0.002 (0.842—0.851)	0.440 $\pm$ 0.005 (0.427—0.448)
<i>D. azteca</i>			
Mexico	4	0.776 $\pm$ 0.003 (0.768—0.784)	0.337 $\pm$ 0.005 (0.327—0.349)
California	4	0.800 $\pm$ 0.004 (0.795—0.812)	0.346 $\pm$ 0.006 (0.331—0.356)
<i>D. melanogaster</i>			
Nebraska	4	0.786 $\pm$ 0.006 (0.781—0.800)	0.438 $\pm$ 0.016 (0.401—0.456)
Texas	4	0.776 $\pm$ 0.003 (0.770—0.782)	0.489 $\pm$ 0.007 (0.476—0.502)
<i>D. narragansett</i>			
New York	4	0.782 $\pm$ 0.005 (0.768—0.792)	0.438 $\pm$ 0.010 (0.421—0.455)
<i>D. pseudoobscura</i>			
British Columbia	4	0.892 $\pm$ 0.007 (0.885—0.899)	0.399 $\pm$ 0.003 (0.394—0.404)
Mexico	4	0.870 $\pm$ 0.003 (0.863—0.876)	0.371 $\pm$ 0.004 (0.368—0.374)
<i>D. tolteca</i>			
Mexico	4	0.753 $\pm$ 0.007 (0.736—0.771)	0.371 $\pm$ 0.017 (0.352—0.386)
Bolivia	4	0.742 $\pm$ 0.008 (0.728—0.761)	0.350 $\pm$ 0.007 (0.338—0.365)

to the head diameter measurements. The females definitely exhibited greater amounts of red pigment than did the males; therefore, this would indicate that the pigment content was dependent upon the head diameter within a given strain of flies since females also had greater head diameters.

The foregoing results indicate a relationship between the head diameter and the total red pigment content of the eye. The pigment content variable was examined for its dependence upon the independent head diameter by utilizing a t-test. The regression coefficients for strains are given in Table III along with their t-values, and the

TABLE II.—The means for head diameter in mm and extinction of the red pigment extract are given for the females of the laboratory strains that were tested; the number of samples (n) is indicated

Laboratory strains	n	Head Diameter	Extinction at 485 m μ
<i>D. affinis</i>			
Missouri	4	0.883 $\pm$ 0.006 (0.872—0.898)	0.564 $\pm$ 0.003 (0.556—0.569)
North Carolina	4	0.869 $\pm$ 0.004 (0.857—0.878)	0.470 $\pm$ 0.011 (0.451—0.492)
<i>D. algonquin</i>			
Nebraska	4	0.956 $\pm$ 0.002 (0.952—0.959)	0.527 $\pm$ 0.003 (0.523—0.534)
Minnesota		0.931 $\pm$ 0.004 (0.924—0.941)	0.511 $\pm$ 0.010 (0.493—0.534)
<i>D. azteca</i>			
Mexico	4	0.833 $\pm$ 0.004 (0.825—0.845)	0.382 $\pm$ 0.006 (0.372—0.397)
California	4	0.854 $\pm$ 0.006 (0.838—0.863)	0.387 $\pm$ 0.006 (0.377—0.402)
<i>D. melanogaster</i>			
Nebraska	4	0.840 $\pm$ 0.002 (0.837—0.846)	0.539 $\pm$ 0.009 (0.522—0.561)
Texas	4	0.839 $\pm$ 0.004 (0.833—0.847)	0.565 $\pm$ 0.009 (0.542—0.582)
<i>D. narragansett</i>			
New York	4	0.853 $\pm$ 0.002 (0.848—0.857)	0.515 $\pm$ 0.004 (0.508—0.525)
<i>D. pseudoobscura</i>			
British Columbia	4	0.936 $\pm$ 0.008 (0.920—0.951)	0.438 $\pm$ 0.006 (0.427—0.448)
Mexico	4	0.918 $\pm$ 0.004 (0.911—0.928)	0.416 $\pm$ 0.004 (0.405—0.422)
<i>D. tolteca</i>			
Mexico	4	0.826 $\pm$ 0.007 (0.804—0.836)	0.479 $\pm$ 0.014 (0.443—0.506)
Bolivia	4	0.814 $\pm$ 0.007 (0.786—0.837)	0.426 $\pm$ 0.013 (0.392—0.454)

significance of the t -values is indicated. All t -values are significant at the 1% level. Undoubtedly the relationship was not the same for each of the strains that was tested or, consequently, the strains with the largest head diameter would also have been those with the greatest pigment content and vice versa. This point was put to test by applying analysis of covariance to see if the regression lines of the different strains might perhaps be parallel. This was found not to be the case; therefore, any adjustment of red pigment content values would be somewhat superficial and might tend to exaggerate the differences that occur.

TABLE III.—The regression coefficient, b , of the red eye pigment variable on the head diameter variable is given for each laboratory strain in addition to the correlation coefficient, r ; the significance of b is indicated by t -values; all of which are significant at the 1% level

Laboratory strains	r	b	t
<i>D. affinis</i>			
Missouri	0.967	1.34	9.57
North Carolina	0.975	1.41	10.85
<i>D. algonquin</i>			
Nebraska	0.980	1.03	13.21
Minnesota	0.953	0.86	7.75
<i>D. azteca</i>			
Mexico	0.896	0.75	4.17
California	0.941	0.76	6.91
<i>D. melanogaster</i>			
Nebraska	0.970	1.86	16.20
Texas	0.886	1.11	4.63
<i>D. narragansett</i>			
New York	0.895	0.83	4.88
<i>D. pseudoobscura</i>			
British Columbia	0.855	0.71	3.94
Mexico	0.723	0.51	3.64
<i>D. tolteca</i>			
Mexico	0.989	1.48	16.44
Bolivia	0.968	1.02	9.27

Upon making intraspecific comparisons of red eye pigment content, one finds what appears to be striking differences between the Missouri and North Carolina strains of *D. affinis* and the Nebraska and Texas strains of *D. melanogaster*. The differences within *D. algonquin*, *D. azteca*, *D. pseudoobscura*, and *D. tolteca* appear to be slight, and dissimilarities in size may account for any differences which might be present in the latter group; however, the diversity of the strains of *D. affinis* and *D. melanogaster* cannot be explained on this basis. *D. affinis* and *D. melanogaster* in this instance could be used to support the theory of polygenes which affect *Drosophila* eye pigmentation as proposed by Nolte (1959).

A comparison of species reveals that all species of the *D. obscura* group tested possess less red eye pigment than *D. melanogaster*, and that the values are more or less closely grouped. Patterson and Mainland (1944) are of the opinion that *D. tolteca* is more closely related to *D. azteca* than to any of the other members of the *D. affinis* subgroup, and this is borne out by examination of the data of head size and pigment content. Any other conclusions of this sort are purely speculative although there is some indication of a similarity of *D. affinis* and *D. narragansett*; however, the diversity exhibited by the two strains of *D. affinis* and the fact that only one strain of *D. narragansett* was tested make this a weak point. *D. algonquin* is the largest member of the *D. affinis* subgroup but it possesses no more red pigment than *D. affinis* or *D. narragansett* but has more red pigment than the less related *D. pseudoobscura*, although *D. pseudoobscura* individuals are much the same size.

Geographical distribution was not revealed to play any great role in pigment content differences in this investigation. There was a slight indication that northern strains tended to have greater head diameters at the temperature at which the flies were raised (18 C). It is possible that the genetic constitution of the northern strains favored growth at the relatively low temperature at which this investigation was conducted.

It is a reasonable assumption that the red eye pigments are by-products of metabolism and are at least in part dependent upon the rates of metabolism. Several observations make any general statement of the relationship impossible. As mentioned earlier in the paper Ephrussi and Herold (1944) demonstrated that the eye pigment content of wild-type *D. melanogaster* increases when the culturing temperature is reduced. Likewise, the rate of development of the flies is also decreased. Moreover, Ephrussi and Herold (1945) showed that the pigment content of the *D. melanogaster* mutant, blood, exhibited an increased pigment concentration at lowered temperatures. Nevertheless, in a limited number of observations by the author the mutant, honey, which is one of the pseudoalleles of the white locus as is blood, possessed less eye pigment at 16° C than at 25° C. This does not refute the work on blood but does indicate that the block in pigment synthesis of the two mutants may be affected differently by changes in the environmental temperature. Rasmuson, Green, and Ewertson (1960) have indicated that the block in pigment synthesis at the apricot locus is probably at an early step and it is likely that the influence of the blood and honey mutants are not far removed.

Considering the wild-type strains dealt with in this paper, the metabolic rate of *D. melanogaster* is greater as evidenced by its shorter developmental period which was 14 days as compared to 17-18 days for the members of the *D. obscura* group. Consequently, it cannot be stated that a reduction in the rate of the developmental processes stimulates a higher rate of pigment deposit or the members of the

D. obscura group would outrank *melanogaster* in red eye pigment content due to their longer developmental period. Hubby and Throckmorton (1960) have courageously attacked this problem from an evolutionary aspect, but in addition much more research is needed at the genetic level.

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Laboratory Life History of the Eastern Harvest Mouse¹

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ABSTRACT: The gestation period of *Reithrodontomys h. humulis* appears to be approximately 21 days. The sizes of nine litters born in the laboratory ranged from two to four, with a mean of 3.2. A mean of 1.2 grams was recorded from the weights of 27 young at birth. The reproductive efficiencies of two females were 50.4 and 50.8 per cent, close to the highest known reproductive efficiency of any mammal.

Harvest mice at birth appear unpigmented, are pink, have a translucent skin, and have tiny, white natal hairs present on most parts of the body. By the end of the first week, the brownish hair on the head and nape almost completely hides the underlying skin. All young are weaned by the end of the third week and are cared for only by the female parent. Parent mice occasionally killed and ate their young, and on one occasion two 30-day-old females were killed and eaten by their two litter mates. Males get along well with females, although males rarely tolerate each other in the same cage. Females are exceedingly tolerant of members of their own sex.

The Eastern harvest mouse, *Reithrodontomys humulis humulis* (Audubon and Bachman), is one of the world's smallest rodents. It is distributed throughout the grasslands and old fields of much of the Southeast; and, although it occupies this extensive range, nowhere has it been found to be locally abundant (Hall and Kelson, 1959). A detailed study on the life history of the Eastern harvest mouse was nonexistent until Layne (1959) published an account of growth and development. Wherever possible, the results of the present study are compared with those reported by Layne (1959).

Audubon and Bachman (*circa* 1854) were the first to give an account of behavior and reproduction of the Eastern harvest mouse in captivity and to describe the type of habitat and ecologic relationships in which these mice were to be found. A captive female, on two occasions, gave birth to young; the first litter consisted of four young, the second of three. Brimley (1923), in a list of breeding dates of mammals found at Raleigh, North Carolina, comments that harvest mice bear from two to five in a litter and live in nests. The first account of daily growth and development of *Reithrodontomys h. humulis* was by Holding and Royal (1952). Developmental changes,

¹ The work reported here constituted part of the requirements for the M.S. degree in Animal Ecology at N. C. State College, Raleigh. I express my sincere gratitude to Dr. Frederick S. Barkalow, Jr., chairman of my graduate committee, for his helpful advice and direction.

² Operated by Union Carbide Corporation for the U.S. Atomic Energy Commission.

behavior, and measurements were recorded for a single survivor of a laboratory-born litter of two.

In this study a laboratory colony of Eastern harvest mice was maintained to study growth and development of young by recording daily weights, measurements, and developmental changes. Also, observations were made of feeding habits, food acceptance, care of young, and other behavior. All mice other than those born in the laboratory were live-trapped from fields at Raleigh, N.C.

MATERIALS AND METHODS

Care of mice.—A laboratory colony of *Reithrodontomys h. humulis* was maintained in cages from March 1958 to April 1959. Usually the colony consisted of 12 to 15 adult mice and one or two litters of young. Although the total number of individuals did not vary appreciably during the period of the investigation, the individual composition often changed due to mortality, escapes, sacrifice of animals, and addition of fresh stocks from the field.

The cages, constructed of $\frac{3}{4}$ -inch wood and faced on one side with $\frac{1}{4}$ -inch mesh hardware cloth, measured 29 by 13 inches in depth, and $16\frac{1}{4}$ inches in height. A nest box was attached to one of the outside walls of each cage. An opening $1\frac{1}{2}$ inches in diameter joined the cage with the nest box 11 inches above the floor of the cage, but easy access to the nest box was provided through use of a 2-inch wide ramp of hardware cloth extending from the cage floor to the nest box. The nest boxes measured $10\frac{1}{2}$ by $8\frac{1}{2}$ inches in depth, and $7\frac{3}{4}$ inches in height. The top of the nest box was hinged to permit removal of the animals from the nest. The floor was concave, forming a depression in the center in which the harvest mice built nests from cotton provided for that purpose.

Weighing and measuring young.—Mice were weighed on a trip balance and measured with a steel rule during the first day after parturition and daily, at the same hour, until 20 days of age. After reaching this age, they were weighed and measured at intervals varying from two to five days until they were 50 days old. The following body measurements were taken: total length, tail length, left hind foot length, and ear length from crown to tip. The total length measurement was taken with the mice resting with the ventral side down rather than in the currently accepted ventral side up position. It was found that the baby mice struggled less and more accurate measurements could be obtained when they were measured in the belly down position. The usual ear notch measurements could not be obtained until the external auditory meatus opened at approximately 10 days of age. It was necessary, therefore, to start with measurements from cranium to ear tip in order to follow growth of this appendage from birth.

Young animals up to 12 days of age could be handled and measured easily, but older more active animals had to be anesthetized

with ether. The amount of ether used was sufficient to render the animal unconscious for about one minute. On two occasions too much ether was used and the mice died.

RESULTS

MATING BEHAVIOR

Mating attempts by captive male harvest mice were observed three times. In the first instance, the male chased the female for about one hour between the nest box and cage. During the entire time the female emitted high-pitched squeals. Several times the male tried to mount the female, but her repulsive action did not permit copulation.

Attempted mating was observed after a female harvest mouse was placed in a cage occupied by a male. The female went into the nest box where she was met by the male, the two touched noses, then cautiously sniffed each other. An attempt by the male to mount the female frightened her to such an extent that she stiffened and did not move. Soon the male gave up his advances and copulation did not occur.

Mating behavior was noted the day after a male and female were placed together in a cage. On this occasion the male chased the female for five minutes, nipping and biting at her tail and hind legs. The female thwarted his mating advances each time an attempt was made.

Evidently none of the described mating attempts was successful, because no young were born to the females after sufficient isolation time. The behavior of the three females indicates that they probably were not in estrus at the time of the observed attempted matings.

GESTATION PERIOD

Layne (1959) reports a 24-day minimum time between successive litters for *R. humulis*; in the present study, postpartum mating was not recorded. Two estimations of the gestation period were obtained.

On May 20, 1958, a female, isolated from other males for several weeks, was placed in a cage with a single male. Twenty-nine days later, this female bore a litter of two. Gestation in this case could have been a maximum of 29 days.

A more precise estimate was obtained when a male was placed in a cage with a female for a two-day period and then removed. Twenty-one days after the male was removed, this female gave birth to a litter of three. Since pregnancy could have occurred on either night the two mice were together, gestation was a minimum of 21 or a maximum of 22 days.

WEIGHTS, LITTER SIZES, AND SEX RATIOS AT BIRTH

The sizes of nine litters born in the laboratory to different mothers ranged from two to four, with a mean of 3.2 (Table I). Layne (1959) reported litter sizes of *R. humulis* to range from one to three, with a mean of 2.2 based upon nine litters.

The average weight of 27 young at birth was 1.2 g which agrees exactly with the mean weight of young reported by Layne. The mean weights of males and females treated separately in the present study did not differ from the mean weight of the sexes combined.

Eight of 11 litters mentioned in Layne's study were born to the same female. This female weighed from 6.5 to 7.0 g (nonpregnant

TABLE I.—Litter sizes, sex ratios, and weights of nine laboratory-born litters of Eastern harvest mice

Litter number	Size	No. ♂ ♂	No. ♀ ♀	Mean weight of young (grams)	Litter weight (grams)	Reproductive efficiency (per cent)
1	3	1	2	1.3	3.9	
2	3	1	2	0.8	2.4	
3	4 ^a	1	1	1.2	4.7	50.5
4	2	1	1	1.3	2.6	
5	3	3	0	1.2	3.6	30.8
6	4	0	4	1.3	5.3	43.1
7	3	1	2	.. ^b	.. ^b	
8	4	1	3	1.4	5.7	50.4
9	3	0	3	1.2	3.6	
Totals	29	9	18			
Means	3.2			1.2	4.0	43.7

^a Sex not determined for two young of this litter.

^b No weights taken at birth.

weight), or about 2.5 g lighter than the weights of the females in the present study. Since reproductive ability varies from female to female, it is possible that the female which produced the eight litters in Layne's study was one capable of having many litters but only a few young per litter. This situation might account for the difference between the average litter size reported here and that reported by Layne. The nine litters of harvest mice from which the data for the present study were obtained were all born to different females. It is apparent that the data of growth and development presented by Layne (1959) should be treated with caution because of the lack of an adequate number in the parental stock.

On four occasions the weight of the mother was taken immediately after the young were born, along with the weight of the litter. The weight of the litter multiplied by 100 and divided by the weight of the mother gives a factor called "reproductive efficiency." Reproductive efficiency is a useful measurement for interspecies and intra-species comparisons. Reproductive efficiencies of 30.8, 43.1, 50.4, and 50.5 per cent were calculated for four individual females. The smallest figure is based upon a litter of three young, whereas the three larger efficiency figures are based upon litters of four young. Most mammals have a reproductive efficiency of 33 per cent or less with the highest

reproductive efficiency of any mammal on record being 53.2 per cent for *Microtus arvalis* (Frank, 1957).

Sex was determined for 27 animals born in the laboratory. Table I shows an unbalanced sex ratio, *i.e.*, 18 females to 9 males. Layne (1959) reported a sex ratio that was even at birth.

PARENTAL CARE OF YOUNG

The care of young is left entirely to the female which, a few days prior to parturition, drives the male from the nest box. The male would usually remain in a corner of the cage until provided with some cotton to build a nest. Sometimes the male himself took cotton from the nest previously shared with the female. During the few days preceding parturition and for a period of about three weeks thereafter, the male remained in his own nest and was not admitted to the nest box. One female allowed her mate to occupy the nest box, but not the same nest that contained the young. The male built a smaller nest a few inches from the maternal nest. After the young started eating solid food, the male would be admitted into the female's nest. One male in Layne's (1959) study occasionally joined his mate in defending the young. Whenever an attempt was made to remove young from a nest to be weighed and measured, their mothers always exhibited defensive behavior. A female would usually scoop the young under her body and commence to bite and push away any object used to obtain the young.

Several of the females would climb up the hardware cloth side of the cage and watch nervously while their young were being handled outside the cage; on the other hand, some mothers would remain quietly in the nest and repair the damage done in extracting the young. Maternal concern for the young diminished soon after the young started eating solid food.

As each baby mouse was returned to the nest, the mother would scoop it close to herself and wash it while manipulating it with her forepaws. The young would try to nurse while they were being washed, but the mother would not permit this until the preening was completed.

If a young mouse was placed a short distance from a nest, the mother would carry it into the nest, grasping the animal at any convenient place on its body with her jaws. The young were sometimes carried by one foot.

The inguinal pair and the two pairs of abdominal teats were the ones usually used for nursing. Only one litter, a litter of four, was known to nurse from the pectoral teats.

Because the mothers exhibited such protective concern for their young, it is hard to understand why they killed and ate so many of them. No less than nine individuals were killed and partially or entirely eaten by one or both parents. One mother killed and partially ate a young mouse that was 31 days old, and another female killed and ate two of her young that were one week old. These two females

had no mates in their cages. The killing and eating of six other young cannot be attributed solely to the female, because the mate was also present. Two 30-day-old females were killed and eaten by their two litter mates. There were no other mice in the cage at the time.

There is no doubt that the mice which were killed and eaten by their parents or litter mates did not first die of natural causes, because all were healthy at least one day before they were found consumed. Sometimes the only trace of a young animal was a tooth or a tuft of hair mixed with the nesting material. Svihla (1931) and Layne (1959) also commented on cannibalism in *Reithrodontomys*.

DEVELOPMENT OF YOUNG EASTERN HARVEST MICE

Eyes.—At birth, the eyes are covered by a semitransparent membrane through which the black iris is visible. By the end of the second day, a slight gray pigmentation on the future eyelids obstructs view of the iris; on the third day faint eye slits can be discerned. Development during the next few days is marked by an increase in pigmentation on the edges of the eye slits, and a deeper ingression of the slit itself. The increased size and subsequent outward pressure exerted by the eye causes a large bulge at the eye location on each side of the head.

The eyelids part from days 9 to 13, and the eye becomes visible. Sometimes, only one eye opens at a time, the opening of the other being delayed until the following day. Eyelids do not part completely until two or three days later. By the end of the second week, the eye resembles a shiny black bead bulging from the head. Further developmental changes are not noticeable.

Ears.—Newborn young have the ear pinnae folded anteriorly and fused with the skin of the head. During the second day and sometimes as late as the third, the ear pinnae become free and extend at right angles to the head, thus exposing the darkly pigmented skin which seals the external auditory meatus. The day after the ear pinnae have been freed, they come to lie close to the head in a more vertical position. At this time, the pinnae are mere fleshy knobs which are colored along the border by dark gray pigment.

The external auditory meatus opens on days 9, 10, or 11, and is followed by rapid development of the fleshy parts of the ear. Also noticeable is an increase in the density of the brown hairs growing along the edge of the ear. The majority of the mice studied by Layne (1959) had open auditory canals on the seventh day, but the opening was delayed as late as 10 days in some of his individuals.

External ear development after the first two weeks is limited to the pinnae becoming slightly ovate as they approach the adult condition.

Digits.—The lateral digits (digits 4 and 5 of each foot) are only partially fused at birth, whereas the remainder are fused from the base of the ill-defined claws to the proximal end of each digit. Usually,

the digits of the forefeet are more fused than their hind counterparts. "Well-separated" digits soon after birth are reported by Layne (1959). The difference in these observations might be attributed to individual variation or possibly to geographic variation. Layne's work was carried out in Florida, the southern limit of the subspecies range on the Atlantic coast, while the author's study was based on specimens from North Carolina, the northernmost state of the subspecies range on the Atlantic coast. Additional work is necessary to clear up these discrepancies.

Pelage.—Young at birth appear unpigmented, are pink, and have a translucent skin. Tiny white natal hairs on the back, neck, and head can be seen with the naked eye, but the hairs of the sides and venter require the use of a hand lens to be seen. All other parts of the body are naked, except the well-developed vibrissae which protrud from the blunt snout.

The dorsum becomes slightly pigmented on the day following birth. The rest of the body remains pinkish. The tail is bicolored due to the dark gray pigmentation on top and pink below. Pigmentation and the density of hairs increase markedly in the mid-dorsal and nape regions, until by the fifth day a brown tinge is conspicuous in the nape region. These changes are paralleled by an increase in the number of white hairs on the venter and on the legs to the base of the digits. Also, first noticeable on the fifth or sixth day is the presence of epidermal scales on the head and back.

At day 7 the brownish hair on the head and nape almost completely hides the underlying skin. The faded pink or almost white color of the belly skin readily shows through the sparse hairs on that part of the body. The skin becomes opaque by the end of the first week of development.

By the eighth day after birth, the brown-gray hairs of the back have covered the sides of the young and form a line of separation where they meet the white hairs of the belly. Sparse white hairs now cover the digits to their distal ends. The epidermal scales of the dorsum and flanks disappear by the eighth or ninth day.

Ten days after birth, the pelage is developed enough to be suggestive of the gray juvenile pelage of most members of the genus *Peromyscus*. The hairs exhibit a sheen and adhere closely to the contours of the body.

An increase in the density of the underfur is distinctly evident in all animals by the start of the second week. The number of guard hairs increases at a slower rate than the underfur hairs. Small traces of the adult ferruginous color usually make their first appearance on day 17 or 18 around the eyes and sides of the young.

During the fourth week, buff colored hairs are prominent on the venter. Also during this period, ferruginous hairs appear higher up on the sides between the forelegs and hind legs.

In further development, the pelage shows a replacement of the grayish juvenile hairs by the ferruginous-brown hairs of the adult.

Usually the rump is the first part of the back to be covered with the adult-type color. Next is the area from the rump to the shoulders. The patch of ferruginous hairs in the eye area gradually enlarges, replacing the gray around the cheeks and extending posteriorly until the molt is completed. A more detailed description of the molt in *Reithrodontomys* is given by Layne (1959).

GROWTH OF YOUNG EASTERN HARVEST MICE

Weight increments.—The daily mean weight increments from birth to 50 days of age for 24 laboratory-born harvest mice indicate an initial fast-growing phase during the first nine days, followed by an abrupt decrease in growth rate on the tenth day (Fig. 1). Daily incre-

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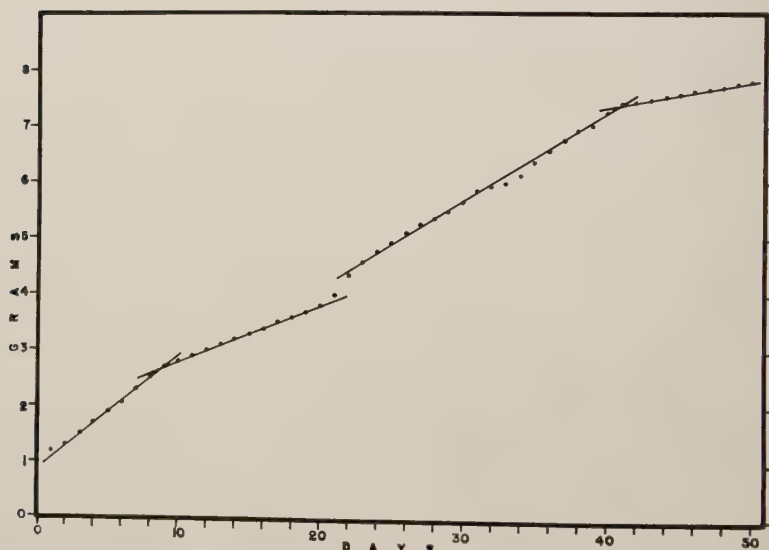


Fig. 1.—Daily mean weight increments showing four separate growth phases from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

ments of about equal magnitude are added from the tenth until about the twentieth day when a third growth phase begins and lasts until the fortieth day. The third growth phase exhibits a slope greater than the second, but not so great as the initial phase. A fourth growing phase, having a very gradual slope, reflects a reduced rate of growth from days 40 to 50. When weighing was discontinued at day 50, mice were still gradually increasing in weight.

During the first growth phase, the young are nurtured entirely on milk of the mother; however, both solid food and milk make up the diet during the second growth phase. Probably reduced lactation and the inability of the young to fully utilize solid food at this time results

in the decreased growth rate between days 9 and 21. A small amount of nursing may still be taking place by the twenty-third day after birth, but by this time the young are usually subsisting on solid food. All young are weaned by the end of the third week.

The ability of the digestive system to utilize fully the nutrients from solid foods is reflected in the increased growth rate from days 23 to 40. After day 40, daily weight increments are much reduced as the animals approach adult weight.

Linear growth.—Growth in total length is rapid for the first two weeks after birth but progressively tapers off during the third, fourth, and fifth weeks (Fig. 2). By the end of the seventh week, daily increments in total length indicate much slower growth.

The growth curves for the left hind foot (Fig. 3) and tail vertebrae (Fig. 4) are essentially parabolic. The hind foot approaches the adult size by the end of the third week. This rapid growth is correlated with other aspects of the biology of the young, for at this time young mice are being weaned and must forage around by themselves in search of food. By the beginning of the fifth week, the growth curve of the hind foot shows signs of being asymptotic. The linear growth of the tail does not begin to level off until the sixth week (Fig. 4).

A sigmoid-type growth curve (Fig. 5) is evident for the daily mean increments in ear length measured from ear crown to tip. The great-

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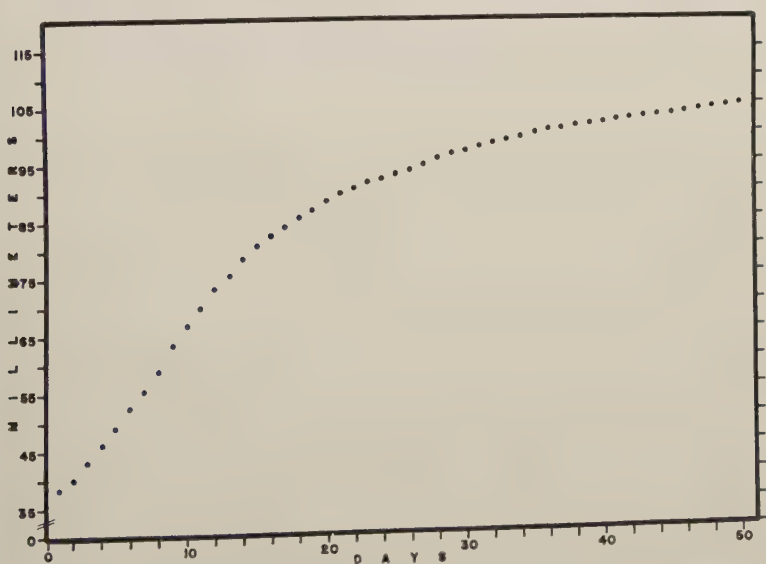


Fig. 2.—Daily mean total length increments from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

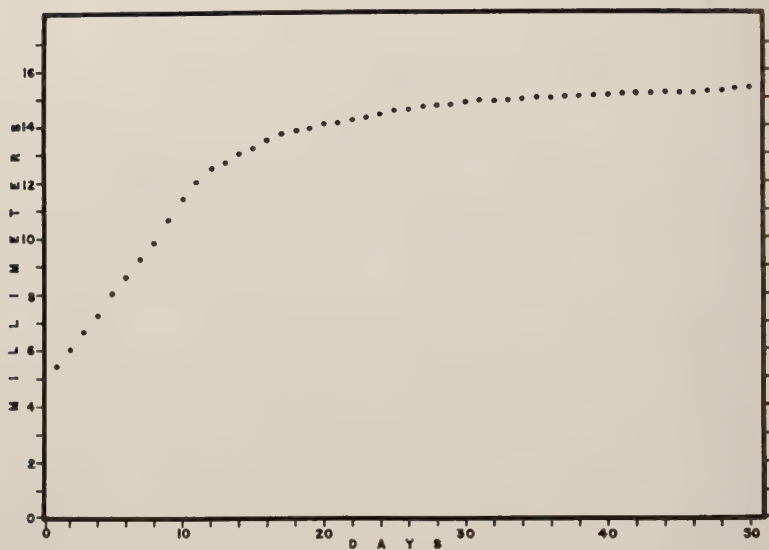
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Fig. 3.—Daily mean length increments of left hind foot from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

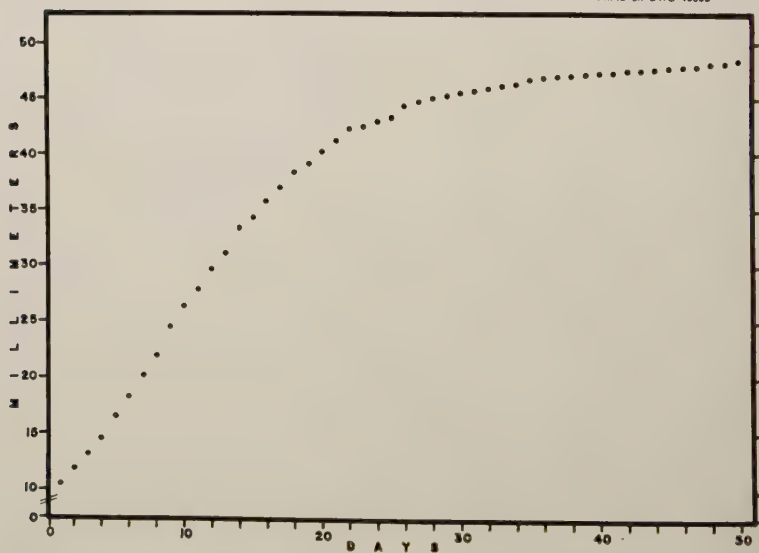
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Fig. 4.—Daily mean length increments of tail vertebrae from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

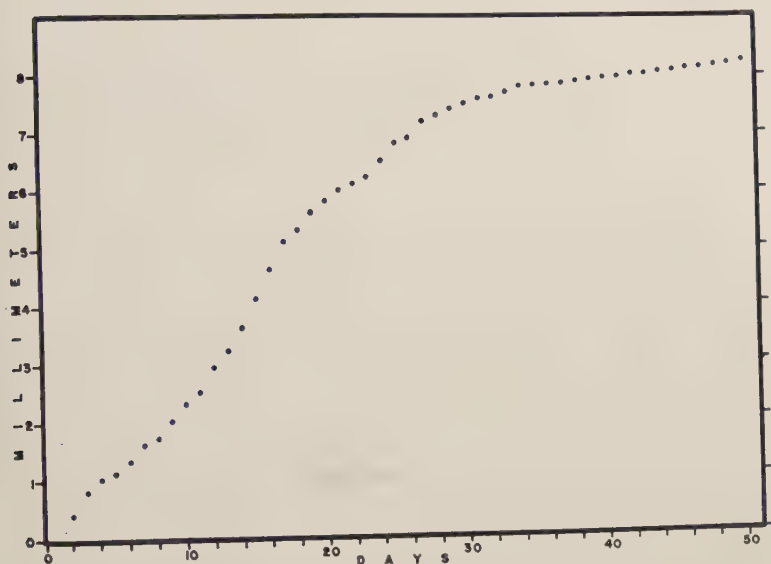
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Fig. 5.—Daily mean ear length increments measured from ear crown to tip from birth to 50 days of age for 24 laboratory-born Eastern harvest mice.

est length increments occur from days 11 to 19 and are followed by a slowing of the growth rate until the increments of the fifth and sixth weeks are but a fraction of the increments during the fast-growing phase.

BEHAVIORAL PATTERNS OF EASTERN HARVEST MICE IN CAPTIVITY

Feeding habits.—The favorite food of laboratory animals was rolled oats. When rolled oats and other foods were mixed and placed in a container within the cage, the rolled oats were always eaten first. Seeds from a lawn mixture of Kentucky blue grass (*Poa pratensis*), red top (*Agrostis alba*), fescue (*Festuca* spp.), perennial rye grass (*Lobium perenne*), and white clover (*Trifolium repens*) were readily hulled and eaten. Mice were also maintained for a long time exclusively on the seeds of Korean lespedeza (*Lespedeza stipulacea*).

Occasionally a piece of apple or other succulent was placed in the cages along with the usual rolled oats or seeds. The succulent material was usually not eaten until after it had become partially dry. This may indicate that harvest mice in the wild obtain water primarily from dew and rain drops and do not utilize succulent vegetation. Other observations point to this too, because pieces of freshly cut green fescue stems and leaves were left untouched but the seeds from the same plants were eaten. Caged harvest mice seemed to prefer to satisfy their thirst by drinking from the water bottles which were always at

their disposal. Fresh fruits and vegetables were fed by Layne (1959) to his colony of Eastern harvest mice.

Harvest mice skillfully pick up tiny seeds in their mouths and transfer them to cupped forepaws. While eating, they sit on their hind quarters, leaving their front legs free for food manipulation. When a piece of rolled oats is being eaten, it is slowly rotated by the forepaws as the edge is chewed off. Rotation continues either until nothing is left or until any small piece which remains is discarded.

Food caches of rolled oats were noted in the corners of cages and nest boxes. This behavior was reported by Layne (1959) only for pregnant females. In the present study, food caches were not restricted to pregnant females.

Sex toleration.—Although males get along well with females, males rarely tolerate each other in the same cage. One instance was recorded in which an adult male killed another adult male on the second day the two were together. During this two-day period, the aggressor continually chased the other mouse about the cage, nipping it around the rump. When the mouse was found dead, it was badly chewed around its hind quarters and tail. Other males were often observed fighting, but none was killed.

Females are exceedingly tolerant of members of their own sex. During a six-week period in the summer of 1958, seven females were housed in one cage. They lived together in a single nest and were always observed to get along well together. When a single male is paired with a single female, toleration before pregnancy is equally as good.

Behavioral variation among individuals.—In general, harvest mice are highly excitable animals. Excited animals exhibited two signs. First there was a noticeable increase in external respiration, probably accompanied by an increased heart beat. Second there was a lateral whipping movement of a much stiffened tail, similar to the way a rattlesnake shakes its rattle. When the tail, moving with rapidity, touched the wooden cage or nest box, the resultant sound was comparable to the muffled noise of a woodpecker pecking on a tree.

Two adult male harvest mice were captured in March, 1958 and maintained for a period of time in separate cages. These two animals exhibited two extremes of behavior. One was very secretive and nervous, while the other was quite tame. The secretive mouse preferred to remain in its nest all day, coming out only at night when no one was in the laboratory. When discovered out of the nest, it would retreat rapidly into the nest box. This mouse would not voluntarily permit itself to be handled and tried to bite at every opportunity. On the other hand, the other mouse was often seen out of its nest during the day. One of its favorite daily pastimes was to perch on the hardware cloth side of the cage for periods of up to two hours with hardly any movements. On one evening it perched on the side of the cage

in a vertical position from 9:30 PM until midnight. This mouse would sit in my hand and allow itself to be petted. No attempts were made to bite or escape.

A third mouse had the habit of hanging onto the hardware cloth side of the cage and gnawing on the galvanized wire. After gnawing from 15 minutes to one-half hour each day for two weeks, it was halfway through the wire when it unexpectedly discontinued the activity.

Sanitation.—Cleanliness is an outstanding trait of *Reithrodontomys humulis*. Toilets were confined to the corners of the cages and were only rarely found in the nest boxes. There was however an occasional voiding of urine in a food tray as a mouse sat eating.

A great deal of time was spent by each mouse in washing and smoothing its fur. Particular care was taken to insure that each hair was glistening and in its proper place.

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Occurrence of Subterranean Isopods in Epigean Waters^{1, 2}

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ABSTRACT: *Asellus stygius* (Packard) was collected at 20 localities in epigean waters of Meade and Jefferson counties, Kentucky. Most observations were made in Doe Run, Meade County, where the species occurred frequently enough in the riffle habitat to be considered a consistent, but minor element of the epigean fauna. The species maintains populations in this environment numbering as high as 43 individuals per square foot.

INTRODUCTION

The occurrence of troglobitic organisms in the epigean environment is generally attributed to accidental displacement (Barr, 1960; and others). This is especially true of the highly modified cavernicolous asellids, with two species, *Asellus tridentatus* (Hungerford) (Leonard and Ponder, 1949; and Dexter, 1954) and *A. conestogensis* (Levi, 1949), being recorded from surface habitats. This paper describes the frequent occurrence of *A. stygius* (Packard) in surface waters of Meade and Jefferson counties, Kentucky. Most of the observations were made in Doe Run, Meade County, with additional material being collected from Otter Creek and "Morgan's Creek," Meade County, and Harrod's Creek, Jefferson County.

Dr. Gerald A. Cole, Arizona State University, assisted in the identification of the specimens of *A. stygius*. Dr. Louis A. Krumholz criticized the manuscript, and he and others of the University of Louisville assisted in the collection of data.

DESCRIPTIONS OF THE STREAMS

The four streams from which *A. stygius* has been collected contrast sharply in physical ecology. Doe Run is a large spring, with an average flow that exceeds 50 cubic feet per second, and with a resultant moderation of temperature extremes throughout. The creek flows primarily over rock substrata for about 10 miles, and enters the Ohio River about four miles upstream from Brandenburg, Kentucky. General descriptions of Doe Run, adequate for the purposes of this report, have been published elsewhere (Cole and Minckley, 1961; Minckley and Craddock, 1961).

The spring originating in Morgan's Cave, herein termed Morgan's Creek, is located in Otter Creek Park, Meade County, Kentucky. The

¹ Contribution No. 44 (New Series) from the Biology Department, University of Louisville, Louisville 8, Kentucky.

² This work was supported in part by the U. S. Atomic Energy Commission under Contract No. AT-(40-1)-2595, with the University of Louisville.

spring is small, with an average flow of about 30 gallons per minute; the spring creek extends for approximately one mile to enter the Ohio River near Rock Haven. The source is located high on a limestone bluff, with the stream descending through broken rubble to pass through a deeply incised, heavily vegetated ravine. The flow of Morgan's Creek is relatively constant. The heavy shade contributes to more or less stable conditions throughout the stream.

Otter Creek, located near Fort Knox, Kentucky, and flowing part of its length through the Fort Knox Military Reservation, is a larger stream than the two mentioned above, and is fed by surface water and small springs along its course. The creek is subject to radical fluctuations in flow, temperature, and turbidity, and these extremes occur much more frequently than in Doe Run or Morgan's Creek.

Harrod's Creek, Jefferson County, is similar to Otter Creek, but is somewhat larger. This stream is located in eastern Jefferson County, and flows directly into the Ohio River upstream from Louisville.

HISTORY OF COLLECTIONS

Asellus stygius was first collected in surface waters near the source of Doe Run in February 1959. At that time no intensive sampling was attempted, and the occurrence was thought to be fortuitous because of the proximity of the spring. On that date, examination of rubble in the mouth of the spring and to about 50 feet downstream produced 19 specimens. Intensive studies of the ecology of Doe Run were initiated in October 1959, and within two months *A. stygius* had been collected at all five of the permanent stations established on the creek, and a number of specimens were obtained at each of four additional localities. At this writing (February 1961), *A. stygius* has been repeatedly taken at the five sampling stations, and the total number of localities on the creek where it has been collected has been increased to 12. This total does not include three collections that were made inside of caves in the drainage. There seems little correlation between the collection sites and the location of caves from which the isopods could have been displaced. The creek basin has been thoroughly explored, thus precluding the occurrence of open caves at unknown places in the drainage; however, the possibility of fissures and undetected springs in the bed of the creek cannot be overruled. The numbers of specimens obtained at some of the localities strongly suggests that some populations are maintaining themselves in the surface environment.

The three additional streams in which *A. stygius* has been collected tend to substantiate the apparent independence of some populations from the true cave environment. The species has been taken in the surface portion of Morgan's Creek on three occasions (four collections have been made in the cave and stream, all of which included specimens from inside the cave). Specimens were obtained twice from the creek about 200 yards above its confluence with the Ohio River, and three times in that portion within 300 yards of the cave. The

records from Otter and Harrod's creeks each are based on single collections. The four small specimens from Otter Creek were all taken beneath the same stone in June, 1960, and two adults were obtained in a similar habitat from Harrod's Creek in October, 1960.

HABITAT AND NUMBERS

In caves, I have found *A. stygius* usually on the under side of flat stones and other debris. Sometimes the species has been seen walking openly on flat rock bottoms and on the walls of solution channels, and it is often found to be most abundant in small solution pools high above the existing water levels in a given cave.

In the surface waters of Doe Run the species is usually found beneath the larger stones on riffles, and in areas that actually approximate the cave environment. However, in many instances, the species was found on rocks less than six inches in diameter, which were loosely associated in relatively swift water. These types of habitat were similar to the areas inhabited by *A. stygius* in Morgan's, Otter, and Harrod's creeks, and are analogous situations to those described for the epigean occurrences of other species (cited above).

Another common habitat in Doe Run, especially in the lower section of the creek, consists of loosely constituted gravels. Thirty specimens were collected in less than half an hour on a gravel bar by carefully digging into the substratum and examining each small stone. The isopods were found to a depth of about six inches, and were typically clinging tightly to the lower surface of the stones, or were deep inside cracks or other irregularities.

The most unique habitat of this species in Doe Run is worthy of a more detailed description. The middle section of the creek includes an area of marl deposition. In this area many of the riffles appear to be bedrock, which, on closer examination, proves to be a recently formed (and currently forming) conglomerate of rubble and gravel cemented by marl. Repeated sampling of this habitat failed to produce any isopods until by chance I broke through the marl slab in the course of sampling with a square-foot Surber sampler. This collection included eight individuals of *A. stygius*. Further examination by hand revealed a large population of the species beneath the slab, and beneath other similar slabs throughout the marl area. In this case it appears that the isopods colonized a "cave" habitat that was formed in the epigean waters.

It is noteworthy that in all cases where *A. stygius* was collected in Doe Run there was consistently a moderate to rapid current and consequent lack of siltation. Specimens kept in containers that were filled with silty water soon became incapacitated. Apparently the suspended particles entangle with the profuse setation, and thus the presence of silt may limit the spatial distribution of the species to areas of pronounced current.

I have no actual quantitative data on the numbers of *A. stygius* in Doe Run per unit area; however, some general estimates may be

made on a "number per rock" basis converted to the number per square foot of rock substratum. The maximum number of individuals found on a single stone was 43 — the stone measured approximately 10 by 14 inches. The average number of specimens for three collections from Doe Run was about four per square foot of surface, with the range from none to 43 (based on the examination of 60 stones larger than six inches in diameter). In the collections made in loose gravel the average number of individuals per square foot was about eight; however, many could have been overlooked. In the latter habitat the individuals averaged smaller in size than in other areas; however, sizes varied from 4 to 10 mm in length (excluding antennae and uropods) at most localities. As noted above, many specimens were taken from beneath marl slabs, but because of the current and the required breakage of the substratum, no estimates can be made as to the numbers present.

Three other asellids occur in Doe Run, and all of these have been taken in association with *A. stygius* at one time or another. These are *Lirceus fontinalis* (Rafinesque), *Asellus brevicaudus* Forbes, and another *Asellus*, which is now under investigation by Miss Barbara A. Walker of this department. The latter form is most abundant in the creek, and has been commonly collected beneath the same rock as *A. stygius* at two of the five permanent stations and at other localities.

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A New Genus of Fossil Salamander from North America

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ABSTRACT: A new genus and species of fossil salamander, *Opisthotriton kayi*, from Niobrara County, Wyoming, Lance formation, Upper Cretaceous, is described. On the basis of the structure of the centrum, *Opisthotriton* is, at present, best regarded as a salamandrid. However, certain features of the available vertebrae exhibit peculiarities encountered in this family as represented at the present time. The genus may eventually be assigned to the *Plethodontidae*, or to an extinct family. Most important is that the recognition of this genus and species establishes the presence of the suborder Salamandroidea in the New World during the Mesozoic. An additional specimen from the Eagle Coal Mine, Bear Creek, Montana, Lower Paleocene is referred to the same genus.

During the past few years several distinctive opisthocoelous salamander vertebrae from the Mesozoic and Cenozoic of North America have come to my attention. Comparison with other known fossil and Recent salamanders indicate sufficient dissimilarity to warrant the description of a new genus. The material constitutes one of the earlier records of fossil salamanders in the world, and provides additional information regarding the composition of the urodele fauna of the Cretaceous of North America.

I wish to thank Dr. M. Graham Netting and Mr. Leroy Kay, Carnegie Museum, for allowing me to study the fossil salamanders in their care, and to Dr. Alfred S. Romer and Mr. Henry Seaton, Museum of Comparative Zoology, for the opportunity of reporting on specimens in that collection.

By far, the most salient single character exhibited by the available specimens is the well-developed opisthocoelous condition of the vertebrae. Only the Salamandridae, and a few genera of the Plethodontidae have vertebrae of this general type.

Soler (1950) has shown that, in the Recent salamanders, opisthocoely may be of two basic types; i.e., (1) "hemicoelous," in which the anterior half of the notochordal canal is solid bone, and (2) "pseudocoelous," in which the notochordal canal is hollow for almost its entire length, but covered anteriorly by an ossified or cartilaginous cap. Partly on the basis of the opisthocoelous condition of the vertebrae Soler resurrected Cope's *Desmognathidae* (Cope, 1866). Moore (1900), on the other hand, had considered opisthocoely as a character of little phyletic value, and had placed Cope's *Desmognathidae* in the *Plethodontidae*.

According to Soler, the *Desmognathidae* includes the Recent genera *Desmognathus* and *Leurognathus*, both of which are hemicoelously opisthocoelous.

Pseudocoelous opisthocoely of the type in which the anterior cap is osseous, occurs in all members of the family Salamandridae, as well as in the Recent plethodontid genus *Thorius*.¹ Pseudocoelous opisthocoely of the type in which the anterior cup becomes covered or filled with a cartilaginous cap or ball, occurs in older specimens of some plethodontid salamanders. However, as indicated by Soler, this is a secondary condition, and quite different from that observed in pseudocoels in which the cap is bony throughout life.

The fossil opisthocoelous vertebrae are provided with a condyle which can hardly be considered to have been cartilaginous in life, due to the absence of any shrinkage of the cap. However, it is possible that under the special conditions of preservation the cap would not have contracted after death as it does in skeletal preparations of recent cartilaginous pseudocoels.

Since the condyle is considered to have been bony in life the question then arises, is the centrum like that found in the hemicelous, or the osseous pseudocoelous types?

By sectioning Recent salamander centra in the median sagittal plane Soler was able to compare the internal structure of the condyle and the notocordal canal. None of the fossil vertebrae were actually sectioned, but one specimen is broken in such a manner that it is possible to see the internal structure of the centrum and the condylar process. The latter is obviously hollow, being covered by a bony (?) cap. The notochordal canal is broad and open for almost its entire length. On this basis the fossils are tentatively referred to the family Salamandridae. However, the possibility still remains that the vertebrae belong to a plethodontid possessing a bony cap, such as that found in *Thorius*. Or, the cap here interpreted as having been bony in life, may have actually been cartilaginous, in which case the vertebrae most closely approach those in some of the Recent plethodontids, such as *Gyrinophilus*. On the other hand, the large size of the fossil vertebrae, as well as certain other characters, may suggest that the fossils should be placed in a new and separate family and not forced into a taxon which will not readily receive it on the basis of our present knowledge.

A number of important studies have been published on fossil urodele remains from Europe, where the earliest salamandrid is reported from the Paleocene. In North America a member of this family has been described from the Oligocene of Oregon (*Palaeotricha* van Frank, 1955). The vertebrae described below are quite different from any previously reported, either from the New or Old Worlds. The material originates from both Cretaceous and Paleocene strata of western United States. It is placed in a new genus:

¹ Cope (1869) had already recognized the peculiar position of *Thorius* in proposing the family Thoriidae. Later (1873) he revised his concept of the entire group and reduced the Thoriidae to subfamily status under the Desmognathidae. In the present paper the recent checklist (Schmidt, 1953) is followed in placing *Desmognathus* and *Leurognathus* in the Desmognathinae.

Opisthotriton n. gen.

Genotype.—*Opisthotriton kayi* n. sp.

Diagnosis.—Vertebrae opisthocelous, larger than any other salamandrid or plethodontid vertebrae known, either fossil or Recent. Hypapophysial keel more strongly developed than in Recent genera of Salamandridae or Plethodontidae. Basipophysial accessory processes strongly developed near the postero-ventral margin of the centrum. As far as is known, similar processes, when present in Recent salamanders, are not located in the same position. Neural arch without the well-developed neural spine observed in many salamandrids, not unlike that in many plethodontids.

***Opisthotriton kayi* n. sp.**

Type.—Carnegie Museum Cat. Vertebrate Fossils No. 6468, a middle trunk vertebra collected by J. B. Hatcher, 1900 (Fig. 1).

Type locality and horizon.—Niobrara County, Wyoming; Lance formation; Upper Cretaceous.

Referred material.—All from the same locality and horizon. Carnegie Museum No. 6466, four fragmentary vertebrae from a smaller individual. Carnegie Museum No. 6468, a complete maxillary, several fragmentary skull elements and two complete atlantes. Museum of Comparative Zoology No. 2813, a single large trunk vertebra.

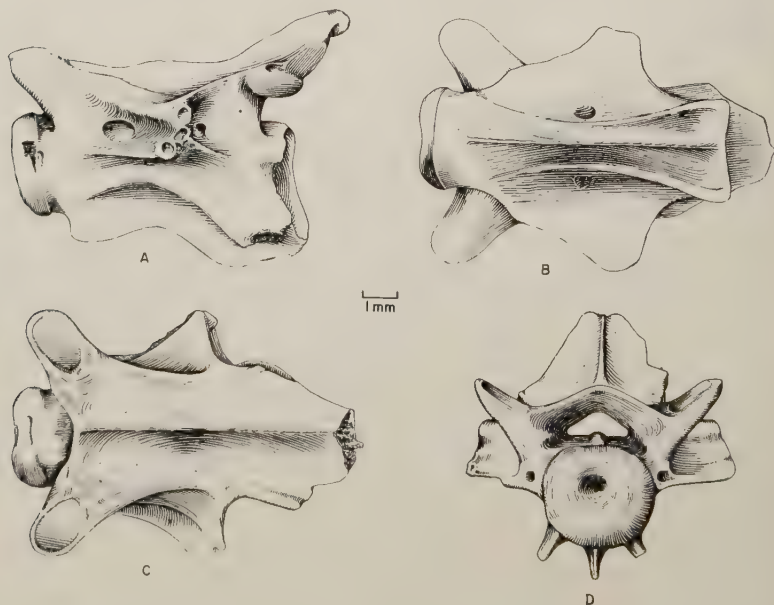


Fig. 1.—Type. *Opisthotriton kayi* nov. gen. et sp., Carnegie Museum No. 6468. A, Lateral; B, Ventral; C, Dorsal and D, Anterior Views. Niobrara County, Wyoming, Lance formation, Upper Cretaceous.

Diagnosis.—As for the genus.

Description.—A middle trunk vertebra (CM 6468) in which the right prezygapophysis and posterior portion of the neural arch are broken away. The measurements (in mm) are as follows: length of centrum along midventral line 8.0; width of the narrowest part of the neural arch from the outer edge of one zygapophysial ridge to the outer edge of the other 3.7; height from the lower margin of the centrum to a line drawn between the outer edges of the prezygapophysial articular facets 4.9.

The vertebra is pseudocoelously opisthocoelous, with a very obvious and well-developed condyle. A notochordal depression is present in the center of the condyle. A median hypapophysial keel is very evident, extending from the anterior to the posterior margins of the centrum. On either side of the hypapophysial keel there are two conspicuous and well-developed basipophysial accessory processes which are best developed posteriorly. Anteriorly they become ridge-like, extending almost to the anterior edge of the hypapophysial keel. A single nutritive foramen is located on either side of the centrum at its union with the base of the transverse process. Condyle circular, flattened antero-posteriorly, with a central depression. Posterior cavity of the centrum rounded, not compressed. Transverse processes broken, but with two distinct rib articulations, connected by a vertical septum. The anterior portion of the lower lamina of the transverse process begins just below and behind the base of the postzygapophysial buttress. It continues posteriorly to near the posterior margin of the centrum. The dorsal lamina is continuous with the interzygapophysial ridges. A large foramen for the vertebralarterial artery is present between the dorsal and ventral laminae of the transverse process just in front of its base. A second foramen, for a spinal nerve, is located just posterior to the base of the transverse process. The prezygapophysial articular facets are oval, directed outwards and forwards from above, and upwards and slightly inwards from the front. The neural arch is depressed, sweeping upwards posteriorly, with a low keel-like neural spine, which is slightly higher posteriorly. The neural canal is low and wide.

Variation.—The four small fragmentary referred vertebrae (CM 6466) provide some information as to both inter- and intra-columnar variation, since their smaller size suggests a different individual than the one represented by the holotype.

All the elements are considerably smaller than the type, and are apparently from an animal about one half the size of the one of which the type vertebra is available. One of these specimens is a middle trunk member. It differs from the type in being much smaller, more obviously depressed, and somewhat more elongate when viewed from above. The hypapophysial keel and the accessory basipophysial processes are less well-developed than in the type. Another vertebra of this series is quite unusual in that the basipophysial accessory processes are extremely well developed. Posteriorly they are twisted

so that their free ends are not parallel with the median sagittal plane. Instead, the flattened, blade-like free ends are directed downwards and backwards, with the flat surface facing downwards and forwards; i.e., they are directed in nearly a transverse plane, though oblique. The free ends of the processes are much longer than in the type, and extend below the ventral lip of the cavity of the cotyle. Whether or not this element represents a vertebrae from near the sacral area is unknown. It might even be a vertebra from the anterior caudal series, although the transverse processes are more like those of the dorsal elements. There is little reason to believe that it represents a second species of *Opisthotriton*, since its peculiarities are simply extensions of a development observed in the type. The chief differences lie in the greater length of the free ends of the accessory basipophysial processes and a flexure of their posterior ends so that they come to be disposed more transversely than parallel to the sagittal plane. Until proven otherwise, the vertebra is best referred to the posterior part of the presacral portion of the column. Similar processes, though located anteriorly on the centrum, are present in the dorsal vertebrae of some caecilians. Their exact function seems unknown, though similar structures in certain extinct amphibians and some fishes are thought to be functionally important in limiting excessive lateral movement. This is particularly important in swimming vertebrates whereby greater efficiency in locomotion is attained by making the body more rigid and thus increasing length of the wave of the swimming movements. Similar structures, though much smaller, and located at the anterior end of the centrum are also found in at least two recent salamander groups; the Sirenidae and the Amphiumidae, both highly specialized for swimming through water. On this basis it is presumed that *Opisthotriton* was a very large aquatic form (to three feet?). The appendicular skeleton was probably reduced. More extensive functional and ecological considerations must await the discovery of a more or less completely articulated skeleton.

The two remaining vertebrae in the series are so fragmental as to preclude comment other than that their general determinable shape indicates they are conspecific with the two small vertebrae briefly described above.

The Museum of Comparative Zoology specimen (No. 2813) is about the same size as the type, but unique in several features, so that it is described in full below. It is here interpreted as an anterior vertebra on the basis of the great development of the hypapophysial keel. The basipophysial accessory processes are less strongly developed than in the type, and the neural spine is higher. The prezygapophyses are not as divergent when viewed from the front or from above.

Unfortunately, the right prezygapophysis and the posterior portion of the neural arch are broken away. As in the type, the vertebra is pseudocoelously opisthocelous, with a well developed condyle. A median hypapophysial keel is very evident. On either side of the keel on the posterior part of the centrum are two conspicuous and well

developed basipophysial accessory processes, which become weaker anteriorly. There are no nutritive foramina between these processes and the median keel. A single nutritive foramen is located on either side of the centrum at its union with the transverse process. The condyle is circular, with a central depression. The posterior cavity, or cotyle, is rounded, not compressed. The transverse processes are provided with two distinct rib articulations, connected by a vertical bony septum. The anterior portion of the lower lamina of the transverse process begins just below the middle of the buttress of the prezygapophysis, and continues posteriorly to near the posterior edge of the centrum. The dorsal lamina is continuous with the interzygapophysial ridges. Two large foramina occur on the centrum between the dorsal and ventral lamina, both immediately anterior and posterior to the base of the transverse process. The prezygapophysial articular facets are apparently oval, directed outwards and forwards from above, and upwards and inwards from the front. The neural arch is depressed, raised upwards posteriorly, with a keel-like neural spine. The neural canal is low and wide. The specimen is illustrated in Figure 2.



Fig. 2.—Museum Comparative Zoology No. 2813, a more anterior vertebra referred to *Opisthotriton kayi* nov. gen. et sp., lateral view. Same locality and horizon as the type.

In addition to the vertebrae mentioned above, two atlantes are available which are referred to this species (CM 6468). In general shape they are less similar to the same element in the Recent Salamandridae than they are to the atlantes of some plethodontids (Fig. 3).

The condylar articulations are rounded and well-separated by a rather thin horizontal septum-like process. The neural arch pedicels are fairly high and narrow; bent slightly medially near their dorsal edge. The neural arch is capacious, being almost as broad as high. The odontoid process is present, though not greatly developed. It is subtriangular from the front, obtusely triangular from the side, and projecting farthest anteriorly near the antero-dorsal edge. The centrum is short, not compressed or with aberrant processes. From below

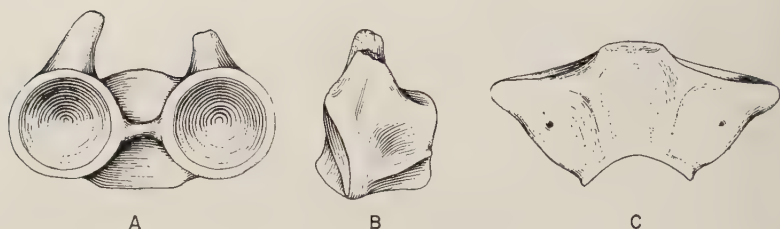


Fig. 3.—One of two available atlantes referred to *Opisthotriton kayi* nov. gen. et sp., Carnegie Museum No. 6468. Same locality and horizon as the type.

it is triangular, broadly truncated posteriorly. The centrum articular cavity produces a definite concave posterior edge on the ventral surface of the centrum. Laterally a slight ridge runs from the ventro-lateral edge of the condylar facet posteriorly and slightly dorsally to the postero-lateral edge of the centrum. The ridge apparently separates the origins of the muscle fibers of the *M. subvertebralis* and the superficial portion of the *M. levator mandibulae anterior*.

An available right maxillary (CM 6468) referred to this genus (Fig. 4) is long and narrow, with the processes of the *pars facialis* located near the anterior end of the element. The anterior parts of



Fig. 4.—Right maxillary, lingual view, referred to *Opisthotriton kayi* nov. gen. et sp., Carnegie Museum No. 6468. Same locality and horizon as the type.

the *pars dentalis* is broken off. The former is roughly trapezoidal in shape and directed slightly anteriorly. At the lingual dorsal border are several knob-like protuberances, separated from the *pars dentalis* by a shallow groove. This groove is more obvious anteriorly than posteriorly. It is here interpreted as the naso-lacrimal duct. The element is provided with fifty-one teeth and/or alveoli. The teeth are shorter anteriorly, gradually increasing in size posteriorly. In cross section they are hollow, and slightly compressed antero-posteriorly.

The tip of a left dentary (CM 6468) is referred to the same species. There are alveoli for eight teeth. There are five foramina in a row on the lingual surface.

Opisthotriton sp.

In addition to the species described above, a second seems represented by a single vertebra (Carnegie Museum No. 6469) from the Eagle Coal Mine, Beartooth Creek, Montana, Lower Paleocene. The specimen is too fragmentary to warrant description as a new species.

As in *Opisthotriton*, the vertebra is opisthocelous and quite large

when compared to most Recent salamanders. It differs from *Opisthotriton kayi* in lacking a well-developed hypapophysial keel, though this structure may have been worn away. The specimen has been badly eroded. The neural arch is depressed, but considerably raised posteriorly. The accessory basipophysial processes are present posteriorly, though they seem to be less well developed than in *O. kayi*. From above the element seems to lack strongly developed interzygapophysial ridges, but these too may have been worn away. In all other regards the specimen is essentially the same as that of the type and referred vertebrae of *O. kayi*.

The opisthocelous centrum and the posteriorly placed accessory basipophysial processes suggest a close relationship to *Opisthotriton*, and the specimen is tentatively placed here until more complete material becomes available. Figure 5 illustrates the vertebra, slightly reconstructed.

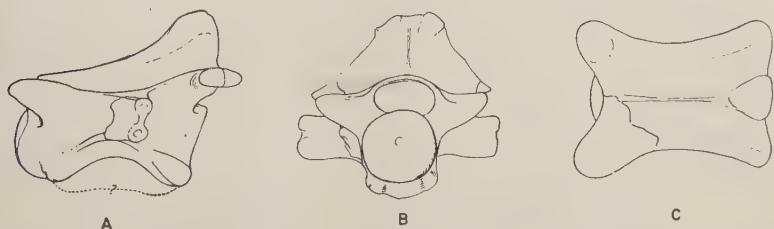


Fig. 5.—A single vertebra (Carnegie Museum No. 6469) from the Eagle Coal Mine, Beartooth Creek, Montana, Lower Paleocene referred to *Opisthotriton* sp.

DISCUSSION

Perhaps the most important single contribution to our knowledge of paleo-herpetology provided by these specimens is the establishment of the presence of the suborder Salamandroidea in the New World during the Mesozoic. However, the familial assignment of the fossils is not definitely established.

Cope (1876) described two genera of urodeles from the Lance, *Scapherpeton* and *Hemityrpus*. The types have apparently been lost, at least temporarily, and the relationships of these two genera are not at all clear. Herre (1950) indeed doubted the existence of any true salamanders in the Mesozoic, placing Cope's genera in the Palaeourodeloidea, a poorly defined group at best. The present material contradicts the view that the true salamanders were not present in the Cretaceous. In addition, Goin and Auffenberg (1957) have shown that the suborder Meantes was already well-established in Lower Cretaceous time.

As pointed out above, on the basis of the structure of the centrum, *Opisthotriton* is, at present, seemingly best regarded as a salamandrid. However, certain features of the vertebrae exhibit peculiarities not

encountered in this family as represented at the present time. The genus may eventually be assigned to the Plethodontidae, or to an extinct family.

The very well-developed hypapophysial keel is one such peculiar feature. A structure of this type, developed to the degree in which it occurs in *Opisthotriton* is, to my knowledge, lacking in all Recent salamanders. It is fairly well-developed in certain highly modified swimming forms, such as *Siren* and *Amphiuma*, but not to the extent that it is in the fossil form. This might suggest that *Opisthotriton* was also a highly modified swimming form. (The importance of the unique keel as a tool in attempting to establish the degree of relationship to any modern group is, at present, unknown.) Of considerable more importance is the fact that the position, and the degree of the development of the accessory basipophysial processes are suggestive of a highly modified aquatic existence, in which efficient swimming played a major role. Herre and Lunau (1950) direct attention to similar structures (incorrectly termed hypapophyses) in *Dehmiella* from the Miocene of Europe. Largely on this basis they place *Dehmiella* in the Plethodontidae, which seems warranted in view of our present knowledge of the osteology of urodeles. Similar processes are found in several genera of plethodontids, including *Eurycea*, *Pseudotriton* and *Desmognathus* among others. The first two are frequently considered as more primitive members of the family. The processes are never found in Recent salamandrids as far as is known. When present in ambystomids, sirenids, amphiumids and even caecilians they are located at the anterior edge of the centrum, and are never as well-developed. *Dehmiella* surpasses all known modern representatives of the Plethodontidae in the development of these structures, though in *Opisthotriton* they are developed even more strongly. *Geyeriella*, from the Paleocene of Europe, a genus considered by Herre (1950) to be a primitive forerunner to the plethodontid salamanders, seems to have these processes very much reduced.

The referred atlantes are relatively simple, and similar to those found in salamandrid genera. They do not possess the aberrant processes found in most plethodontids.

The referred maxillary is considered primitive on the basis of its great length and the more anterior position of the *pars facialis*. The Salamandridae possess longer maxillae than do the Plethodontidae. The anterior opening of what is believed to be the nasio-lacrimial duct in the fossil maxillary is also worthy of comment in that the duct occurs in all Recent salamandrids and plethodontids, with the exception of the Desmognathinae (Wilder, 1913).

Dunn (1926) has postulated that the plethodontid salamanders arose in the New World from a salamandrid stock. The genus *Opisthotriton* (if the tentative familial assignment is correct) represents the earliest salamandrid reported so far. However, it is highly possible that in *Opisthotriton* we have represented a form phyletically intermediate between the two families. The European Paleocene

Geyeriella may thus represent a side line of the main evolutionary sequence leading to the Plethodontidae; which might explain some of its peculiarities. *Dehmiella* seemingly represents the first known true plethodontid and thus conforms with the general phenomenon of faunal "modernization" during the early Miocene.

If the plethodontids originated in the New World from a salamandrid type, and a somewhat intermediate form is present in the Upper Cretaceous, the Salamandridae must represent a very ancient lineage. Fossils of this family, much older than those now available, are thus to be expected.

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Liatris provincialis, sp. nov., (Compositae), Endemic in Western Florida

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ABSTRACT: *Liatris provincialis* is newly described from western Florida. It is allied with the three species of Series *Pauciflorae* and is most nearly like *L. chapmanii*. *L. provincialis*, so far as now known, is restricted to Franklin and Wakulla counties, Florida. (Illustrated.)

Gaiser (1946) in her revision of the North American genus *Liatris* states that of the thirty-two species recognized by her the largest number for a single state, 12, occurs in Florida. Three of the twelve are endemic in Florida: *L. garberi* A. Gray, *L. pauciflora* Pursh, and *L. laevigata* Nutt. *L. garberi* and *L. laevigata* are restricted to peninsular Florida, whereas, *L. pauciflora* occurs generally across the northern part of the state and in the upper peninsula.

The distinctiveness of the plant described below was first noticed when it was observed in great abundance on sand dunes along the Gulf of Mexico between Lighthouse Point and Peninsular Point, Franklin County. There it occurred from the crest of the fore dunes shoreward on more stabilized dunes and into the evergreen oak-sand pine scrub adjacent. This area is a small narrow peninsula more or less paralleling the mainland on the seaward side of Alligator Harbor and is sometimes referred to as Alligator Peninsula. Later the plant was found to occur in evergreen oak-sand pine scrub along the coast from nearby Ochlockonee Bay generally southwestward to Carabelle and a little beyond, a distance of about 30 miles; also on sandy ridges of turkey oak-longleaf pine about two miles back from the coast in this vicinity and for about two miles north of Ochlockonee Bay in the vicinity of Panacea. Diligent search in areas of coastal dunes and evergreen oak-sand pine scrub near the Gulf westward of the Apalachicola River and on sandy ridges of turkey oak-longleaf pine elsewhere throughout the Florida Panhandle failed to reveal any other places of occurrence for this new *Liatris*.

Liatris provincialis Godfrey, sp. nov.

Fig. 1

Liatris chapmanii affinis, sed capitulis (plerumque lato-divaricatis nec anguste adscendentibus) flosculisque minoribus. Cormi variabilis globosi vel ovaes vel unco-elongati. Caules solitarii vel plures ad 8 dm alti simplices vel pauci-vel multiramosi striati dense breviterque

¹ This investigation was supported (in part) by a research grant, RG-6305, to the author from the Division of General Medical Sciences, Public Health Service.

cinereo-pubescentes vel raro subglabri. Folia numerosa in ambitu glabra, inferiora lineari-oblongeolata, gradatim in superiora minora linearia transeuntia. Capitula sessilia vel rarius breviter pedunculata sat distantia plerumque divaricata vel leviter adscendentia ca. 12-15 mm longa plerumque 3-flora. Involucra cylindrica vel subturbinata; phyllariis glanduloso-punctatis apice purpureis margine scariosis et ciliatis, exterioribus ovatis breviter acutis vel longe acuminatis, interioribus lineari-oblongis breviter acuminatis. Pappi setae barbellatae 7-8 mm longae. Corollae tubus 6-7 mm longus, intus leviter pilosus basin



Fig. 1.—*Liatris provincialis*: a, habit; b, small portion of stem with a leaf base; c, head; d, flower; e, portion of flower with corolla slit longitudinally and spread open; f, achene; g, a representative series of phyllaries.

filamentorum verus; lobi 3 mm longi. Achaenia 5 mm longa valde costata pilosa.

HOLOTYPE.—Franklin County, Florida: sand dunes along the Gulf of Mexico, Alligator Point, October 4, 1959, *Godfrey 58985* (deposited in the Gray Herbarium).

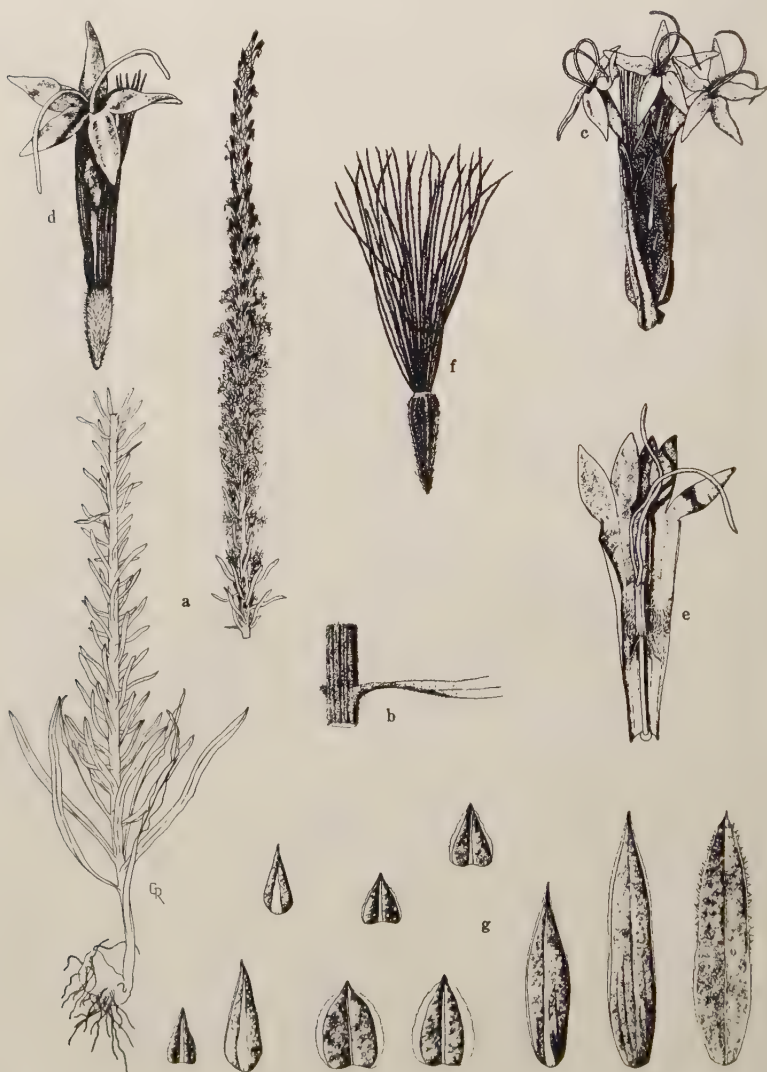


Fig. 2.—*Liatris chapmanii*: a, habit; b, small portion of stem with a leaf base; c, head; d, flower; e, portion of flower with corolla split longitudinally and spread open; f, achene; g, a representative series of phyllaries.

Additional specimens.—*Franklin County*: turkey oak-longleaf pine sand ridge, between St. James and the Ochlockonee River, September 16, 1960, *Godfrey 60282*; *Wakulla County*: turkey oak-longleaf pine ridge, ca. $\frac{3}{4}$ mile N of Panacea, September 16, 1960, *Godfrey 60283*; sandy scrub at Panacea, September 8 - 10, 1955, *Thorne and Davidson 17286*.

Liatrix chapmanii T. and G., (Fig. 2), which this proposed new species most closely resembles, occurs both on sandy ridges of turkey oak-longleaf pine and in some areas of evergreen oak-sand pine scrub throughout the Florida Panhandle (as well as eastward and southward and with a single record for Decatur County in southwest Georgia). I have not ever observed it on coastal dunes nor have I seen it within the very limited range of *L. provincialis* even though, except for the dunes, the two species occupy what appear to be the same habitat types.

Liatrix provincialis appears to be allied with the three species of Series Pauciflorae as delimited by Gaiser (1946) and is more nearly like *L. chapmanii* than to either of the other two, *L. secunda* Ell. and *L. pauciflora*, which are more similar to each other than either is to *L. chapmanii*. The one character possessed by *L. provincialis* which is not given as characteristic of the other members of Series Pauciflorae is that of ciliolate phyllaries. This is not here interpreted as significant in regard to the delimitation of the Series for its members do seem to form a natural group despite this species not having "read the book." As a matter of fact some of the phyllaries of *L. chapmanii* are ciliolate on some specimens.

Superficially and even at a distance *Liatrix provincialis* can be distinguished from *L. chapmanii*. The heads of the former, at full anthesis, extend outward at right angles from the axis and are distant enough from each other so that the inflorescence has a decidedly interrupted appearance. This characteristic is somewhat obscured in pressed and dried specimens but still contrasts with the arrangement of the heads of *L. chapmanii* which are rigidly ascending, appressed to the axis and to each other, overlapping, and make the spike appear as a narrow, continuous cylinder. This difference is striking. The leaves of *L. provincialis* are not pubescent, those of the other are usually abundantly clothed with short stiff hairs. Most of the other features by which the two are distinguished are quantitative characters of the heads and flowers yet these features seem to be constant and some of them relatively large. The heads of *L. chapmanii* are longer (18-20 mm *vs* 12-15 mm) and somewhat broader although the breadth is difficult to specify because it depends at what stage of development the measurement is taken. The pappus is 11 mm long in *L. chapmanii* and 7-8 mm in the other. The corolla tube and lobes of the corolla respectively of *L. chapmanii* are 11 mm and 4 mm long whereas those of *L. provincialis* are 6-7 and 3 mm long. Although the inner phyllaries of the heads of *L. chapmanii* are longer there is

a variability in the shape of the outer ones of both plants, particularly as to the form of their tips and the width of the scarious margins, which makes them of little diagnostic value. Cilia on both the phyllaries and the bracts subtending the heads are more conspicuous and uniformly present in *L. provincialis* than in *L. chapmanii* but this is a matter of degree and cannot be satisfactorily expressed for purposes of distinction.

It may be argued that *L. provincialis* had better be treated infrspecifically with *L. chapmanii*. This, however, may be equally true with regard to certain others pairs of species of *Liatris*, for example, *L. secunda* and *L. pauciflora*, *L. tenuifolia* Nutt. and *L. laevigata*. It appears to me that the most recent revisionary treatment of *Liatris* by Gaiser (1946) is subject to considerable question as to the specific and infraspecific status accorded various taxa. Chromosome counts and chromosome morphology appear not to be very helpful within the Series in this genus as regards assigning status. For instance, chromosome counts made by Gaiser (1950) for taxa in the Series Graminifoliae and Pauciflorae were $n = 10$ for all species and no karyotypic variation was observed which would be helpful in the question of status for the taxa. This is not to belittle Dr. Gaiser's work but suggests that if rank is to be ascertained other than by those criteria thus far employed, it must await investigations of a different kind.

Dr. Lloyd H. Shinnars, Southern Methodist University, provided the Latin diagnosis. His generous aid is gratefully acknowledged. Illustrations were prepared by Mr. Grady W. Reinert. The details illustrated for each of the two species were drawn to the same scale.

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Observations on the Fleas (Siphonaptera) of Some Small Mammals in Northwestern Illinois

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ABSTRACT: The relative infestation of small mammals by fleas was studied in northwestern Illinois. Eleven host species numbering 718 individuals were collected from February to October in 1958. Three hundred eighty-six fleas of 11 species were taken from these hosts. More fleas per host were collected in the cooler months than in the warmer months. *Orchopeas leucopus*, a flea often considered to infest *Peromyscus* without exhibiting an apparent preference as to species, may actually be more common on species which occupy woodland habitats. Mean numbers of fleas of each of three species on *Peromyscus leucopus*, a host species taken in all seasons, indicated that peak populations of the three species do not coincide.

A relatively large number of shrews and associated small mammals were trapped during a survey for rabies in shrews between February 14 and October 3, 1958. Fleas were removed from these specimens and submitted for identification to the Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey. Because relatively little is known about fleas in this section of the Midwest these records are believed to represent a contribution.

Acknowledgment.—These observations were supplementary to an investigation of sylvan rabies which was supported by a grant (No. E-1349) from the Division of Research Grants, U. S. Public Health Service, Department of Health, Education, and Welfare. Thanks are due Dr. C. O. Mohr for suggesting the study and for a critical reading of the manuscript and to Dr. L. J. Stannard for identifying the fleas. Also, Drs. T. G. Scott and R. E. Yeatter, and Mr. G. C. Sanderson gave help and advice which is gratefully acknowledged.

METHODS

Ninety-five trap lines, each consisting of 20 stations 10 yards apart with two break-back traps per station, were set along secondary road rights-of-way in Jo Daviess, Carroll, and Whiteside counties. The traps, baited with liver sausage to attract shrews, were allowed to remain in place for two consecutive nights. The traps were examined each morning, captured animals removed, and the bait replaced when necessary. Specimens obtained were placed in individual No. 1 paper bags.

In the laboratory, the contents of each bag were dumped into the center of a piece of brown wrapping paper. The sack was torn apart, and fleas clinging to the bag or to debris were collected with forceps and placed in a vial of 70 per cent alcohol. The mammal carcass was then brushed and combed thoroughly with the points of the forceps, and additional fleas clinging to the host were collected. Mammals which were badly deteriorated or partially eaten by other animals were not examined for fleas.

TABLE I.—Numbers of each species of hosts examined for fleas and numbers of each species of fleas with which the hosts were infested in northwestern Illinois, February 14-October 3, 1958

Host Species	Number hosts examined	Species and Numbers of Fleas											Totals
		<i>Orchopeas leucopus</i>	<i>Epitedia weinmanni</i>	<i>Ctenophthalmus pseudagyrtes</i>	<i>Nearctopsylla genalis</i>	<i>Opisocrostitis bruneri</i>	<i>Megabothris asio</i>	<i>Monopsyllus wagneri</i>	<i>Oropsylla arctomys</i>	<i>Corrodopsylla curvata</i>	<i>Stenoponia americana</i>	<i>Doradopsylla blarinae</i>	
<i>Microtus pennsylvanicus</i>	164	1	13	13			7	1	1	1			37
<i>Microtus ochrogaster</i>	69	1	5	11			2				2		21
<i>Peromyscus maniculatus</i>	115	8	10	6				16					40
<i>Peromyscus leucopus</i>	179	91	19	3				51					164
<i>Blarina brevicauda</i>	125		4	48	1		1	2		48		3	107
<i>Reithrodontomys megalotis</i>	15	2						1					3
<i>Sorex cinereus</i>	16			1									1
<i>Mus musculus</i>	19							3					3
<i>Citellus tridecemlineatus</i>	8					5							5
<i>Zapus hudsonicus</i>	6							2					2
<i>Mustela vison</i>	2		3										3
Totals	718	103	54	82	1	5	10	76	1	49	2	3	386

OBSERVATIONS

Of 790 hosts captured, 718 were examined for fleas. Three hundred eighty-six fleas, representing 11 species, were collected. The species and numbers of hosts and fleas are shown in Table I.

Orchopeas leucopus (Baker) was the most numerous of the fleas collected; 103 were taken. Although five species of hosts were infested, 99 of the specimens were obtained from *Peromyscus*. In New York, Benton and Cerwonka (1960:389) collected this species with about equal frequency from *Peromyscus leucopus* (Rafinesque) and *Peromyscus maniculatus* (Wagner). In northwestern Illinois, more than seven times the number of *O. leucopus* per host were taken from *P. leucopus* than from *P. maniculatus*. In this area, *P. maniculatus* is represented by the form *Peromyscus maniculatus bairdii* (Hoy and Kennicott) which inhabits grassland and open fields, and tends to be ecologically separated from *P. leucopus* in most habitats. In New York, *P. maniculatus* is most often represented by the form *Peromyscus maniculatus gracilis* (Le Conte) which is an ecological associate of *P. leucopus* (Hamilton 1943:271). It may be that woodland is a more suitable habitat for this species of flea, and *P. maniculatus* is commonly infested only where the habitat is such that it is closely associated with *P. leucopus*. Mohr (1956:390) believed that suitability of habitat to chiggers (Acarina) in New Guinea was more important in determining the rates of infestation per host than was preference exhibited by the ectoparasites for a specific host. Layne (1958:6) listed *O. leucopus* from *P. leucopus* and *P. maniculatus* taken on strip-mined land (at Pyatt) in southern Illinois where in many situations these hosts are closely associated (Verts 1957:56).

The mean number of *O. leucopus* on *P. leucopus* was 0.2 or fewer per individual in February and April but reached a peak of 2.0 per individual in May. The mean number per specimen declined to the previous level in the summer months (June-August) but increased to about 0.6 per host in October (Fig. 1).

Ctenophthalmus pseudagyrtes Baker was the second most common species of flea collected. Six species of mammals were infested (Table I). More than half of the specimens were collected from short-tailed shrews, *Blarina brevicauda* (Say), and more than twice as many fleas per specimen were obtained from this host as from any other. Benton and Cerwonka (1960:388) consider this species of flea to be one of the less host specific. From February to June, when 15 or more *Blarina* were examined per month, the mean number of *C. pseudagyrtes* per individual fluctuated between 0.2 and 0.5. The rate of infestation tended to be greater in the warmer months. Too few *Blarina* were captured in the other months to obtain comparable data.

Monopsyllus wagneri (Baker) was the next most commonly collected flea. Seventy-six specimens were obtained from seven species of mammals (Table I). More than 88 per cent of the specimens were taken from *Peromyscus*, but about twice as many per host were found

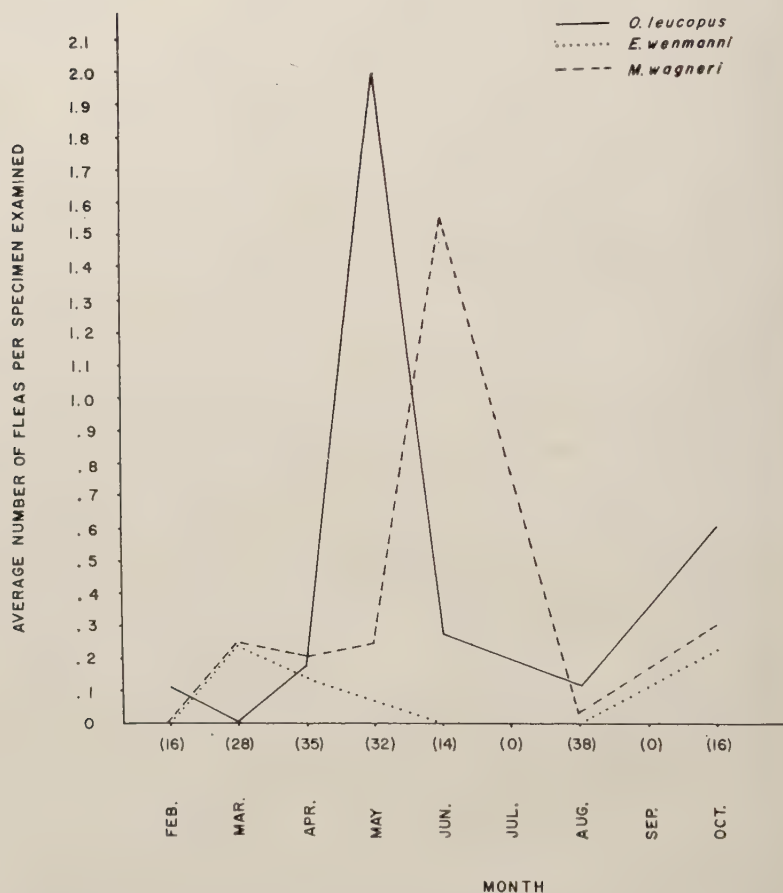


Fig. 1.—Mean numbers of three species of fleas collected from *Peromyscus leucopus* each month, February-October, 1958. (Numbers in parentheses indicate numbers of hosts examined.)

on *P. leucopus* as on *P. maniculatus*. On *P. leucopus*, the mean number of this species per host was about 0.3 in March, April, and May (Fig. 1). In June, when 14 *P. leucopus* were examined, 1.6 fleas per host were collected. Only 0.03 per host were collected from 38 specimens examined in August, but there was an increase to slightly above the pre-June level of infestation in October. More *M. wagneri* were also collected from *P. maniculatus* in June than in other months.

Epitidia wenmanni (Rothschild) was collected from six species of mammals (Table I). Fifty-four specimens were taken, 29 from *Peromyscus*. The mean number per host was nearly equal on *P.*

leucopus and *P. maniculatus* (about 0.1); the rate of infestation was slightly less on *Microtus pennsylvanicus* (Ord) and *Microtus ochrogaster* (Wagner). On *P. leucopus*, from which about one-third of these fleas were obtained, a mean of 0.3 per host was collected in March. There was a gradual decline in mean numbers per host in April and May; none was taken in the summer months. The mean number per *P. leucopus* in October was the same as that in March. Although fewer were collected from *P. maniculatus*, a similar seasonal trend in the rate of infestation was evident.

Corrodopsylla curvata (Rothschild) was found only on *B. brevicauda* and *M. pennsylvanicus*; 48 were collected from the former, 1 from the latter. Holland (1949:95) reported that this species was often associated with *Sorex*. The 16 *Sorex cinereus* Kerr examined were not infested (Table I). No *C. curvata* were collected from *Blarina* in February and March. From April to June there was an increase from 0.4 to 0.7 per specimen. Although this flea was collected from *Blarina* in July, August, and October, too few hosts were examined to provide comparable data.

Of the remaining six species of fleas infesting the small mammals, 10 or fewer of each were collected (Table I). *Opisocrostis bruneri* (Baker) and *Doratopsylla blarinae* C. Fox, host specific for *Citellus* (Jellison 1947:64) and *Blarina* (Benton and Cerwonka 1960:389), respectively, were taken only from their respective hosts. One *M. pennsylvanicus* bore a single *Oropsylla arctomys* (Baker), a flea which is usually associated with woodchucks, *Marmota monax* (Linnaeus), (Benton and Cerwonka 1960:389). *Megabothris asio* (Baker) and *Stenoponia americana* (Baker) were also found on *Microtus*; a single specimen of the former flea was taken from *Blarina*. A single *Nearctopsylla genalis* (Baker) was taken from *Blarina*.

DISCUSSION

The relatively large numbers of different species of fleas collected from *Blarina* (7) and *Microtus* (8) are probably a reflection of the habits of the two species. Tunnels constructed by *Microtus* are extensively used by *Blarina* and other small mammals, which affords ample opportunity for exchange of fleas between host species. Fleas which occurred in relatively large numbers on *Microtus* (*Megabothris asio*) and *Blarina* (*Ctenophthalmus pseudagyrtis* and *Corrodopsylla curvata*) were occasionally interchanged (Table I).

Adequate numbers of *P. leucopus* were taken in all seasons to permit comparison of relative abundance of three species of fleas with which they were infested. There appears to be a seasonal difference in the rates of infestation by these fleas. *E. wenmanni* was more common in March and October, but less so in spring and summer; *O. leucopus* was more than three times as abundant in May as in any other month; *M. wagneri* was nearly four times as abundant in June as in any other month (Fig. 1).

The small number of fleas of all species collected from *P. leucopus* in August, when more were examined and the rate of capture per unit effort was the highest, may be a result of fleas leaving the dead hosts after the carcasses had begun to cool. This may be less likely in winter when the insect parasites would tend to be immobilized by cold.

The mean number of all species of fleas infesting all species of mammals increased from February to June. Although fewer mammals were examined in July, August, and October than in other months, there appeared to be a decline in mean numbers per host in the warmer months followed by a slight increase in October.

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Wintering Distribution Changes in Mallards and Black Ducks

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ABSTRACT: Through the use of data compiled by the Audubon Society's annual Christmas Counts, an attempt has been made to trace the distributional changes of wintering Mallards and Black Ducks in the eastern states from 1900 to the present. During this period the Black Duck has increased relative to the Mallard in few if any states (the Great Lakes region), whereas the Mallard has increased nearly everywhere else (except in the extreme northeast), particularly in the southern coastal states. Deforestation and changes in land use are suggested as probable reasons for this trend, which is not likely to be reversed.

Although several rather spectacular shifts in the distributions of various American species of birds have become evident in recent years, the "colonization" of the eastern states by the Mallard (*Anas platyrhynchos*) has not been so generally recognized. The magnitude of this range extension has been great nevertheless, and the probable reasons for it have been discussed elsewhere (Johnsgard, 1959, 1961). Concomitant with the increase of the Mallard in the eastern states, the native Black Duck (*Anas rubripes*) has suffered a decline in numbers, and apparently for some of the same reasons as the Mallard has increased. Since this trend is not likely to be reversed in the future, it will be of interest to follow it carefully and thus possibly to predict the fate of the Black Duck.

Wing (1943) became interested in the ratios of Mallards to Black Ducks throughout the eastern states before the range shift was at all apparent, and calculated state ratios for the two forms on the basis of the data provided by the annual Audubon Society Christmas counts for the forty years 1900 to 1939. He found that the average ratios for that period (which, because of the continuously increasing number of counts, is probably typical of the situation somewhat after the mid-point of 1920) indicated that the zone of equal ratios fell in a north-south line between Michigan and western Florida. East of this line the Black Duck was markedly dominant over the Mallard and west of it the Mallard was equally dominant. Wing's data are presented in Table I, but they are converted from simple Mallard: Black Duck ratios to the alternative method of calculating the relative percentages of each form in the combined sample. This latter means of presenting ratio data has certain statistical advantages (Hickey, 1957). Arguments supporting the use of these data as unbiased estimates of wintering Mallard and Black Duck populations have been presented elsewhere (Johnsgard, 1959), and so will not be repeated here.

To test the possibility that these counts might indicate the degree to which the Mallard has moved eastward in recent years, it was de-

cided to bring these calculations up to date, by collating the Christmas Count records for the twenty years 1940 to 1959. Since the numbers of counts and counters has increased enormously since 1940, the data were divided into earlier (1940-1949) and later (1950-1959) periods. Again, although the averages for these total periods are presented (Table I), they probably reflect the existing conditions somewhat after the mid-points of the periods. It must be remembered too that changes in the ratios can be attributed both to Mallard increases in the East and to Black Duck decreases, rather than only to Mallard increases alone.

The data for the years 1940 to 1949 show some interesting differences from Wing's data for the preceding forty years. Of the states east of the Michigan to western Florida zone, one state (Florida) exhibits a majority of Mallards in the wintering population. Fourteen states exhibit what are probably significant reductions in the percentages of Black Ducks, with the most marked changes occurring in Florida, North Carolina, and Michigan. Only four states (Wisconsin, Kentucky, West Virginia and Virginia) exhibit noticeable increases in Black Duck ratios; of these West Virginia's data are probably not based on a sufficient sample. Since Wing's (1943) data did not include information on sample size it is impossible to evaluate these differences statistically.

The data for the years 1950 to 1959 bring to light some even more striking changes. Five states (Florida, Georgia, South Carolina, North Carolina and Ohio) east of the Michigan-western Florida zone exhibit majorities of Mallards in the samples. Eighteen states exhibit marked declines in Black Duck ratios from those presented by Wing. Only two states (Minnesota and Wisconsin) exhibit significant increases in Black Duck ratios over those of preceding years.

To provide a relatively up-to-date picture of the situation, data for the years 1958 to 1960 are also presented in Table I. Although in some cases the sample sizes are too small to be useful, in most a still greater decrease in Black Duck ratios is evident. It is astonishing to contemplate that in twenty years Delaware, for example, has undergone a shift in ratios from an almost pure Black Duck population to one in which Mallards are more abundant than Black Ducks. Other only slightly less remarkable examples are provided by the coastal states from North Carolina to Florida. On the other hand, the northern interior states have undergone less pronounced decreases, such as, for example, Michigan, Illinois, Indiana and Ohio. If a line delineating the zone of equality between Mallard and Black ratios were to be drawn today, it would still have to pass through Michigan at the north, but be deflected eastward to the south so as to pass through Virginia and North Carolina. Only in Maine and the Canadian maritime provinces may the wintering population still be considered "pure" Black Duck. It appears, therefore, that the Mallard has been invading the East by a "flanking" movement along the Gulf Coast states. It is hard to determine how rapidly the Mallard has colonized

TABLE I.—Relative numbers of wintering Mallards and Black Ducks, based on Audubon Christmas Counts from 1900-1960

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
Nova Scotia			
1950-1959	5,962	2	99.97
1958-1960	1,865	1	99.95
Quebec			
1940-1949	2,092	81	96.27
1950-1959	6,314	155	97.60
1958-1960	1,821	50	97.33
Ontario			
1900-1939	-----	-----	97.51
1940-1949	9,370	1,450	86.59
1950-1959	15,163	7,936	65.36
1958-1960	7,261	3,793	65.69
Maine			
1940-1949	1,773	2	99.89
1950-1959	6,543	43	99.35
1958-1960	5,102	29	99.43
New Hampshire			
1950-1959	5,791	171	97.13
1958-1960	1,736	234	88.12
Vermont			
1940-1949	272	11	96.11
1950-1959	538	12	97.82
1958-1960	170	5	97.14
Massachusetts			
1900-1939	-----	-----	99.28
1940-1949	78,570	472	98.52
1950-1959	117,499	7,002	94.37
1958-1960	53,679	4,606	90.38
Rhode Island			
1900-1939	-----	-----	99.35
1940-1949	18,468	101	99.45
1950-1959	18,759	410	97.86
1958-1960	6,800	221	96.85
Connecticut			
1900-1939	-----	-----	94.31
1940-1949	19,398	577	97.11
1950-1959	39,802	13,646	74.47
1958-1960	15,269	8,838	63.34
New York			
(entire state)			
1900-1939	-----	-----	96.12
1940-1949	135,376	13,426	90.97
1950-1959	202,713	30,563	86.90
1958-1960	65,891	14,417	82.05

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
New York			
(Long Island)			
1940-1949	78,172	4,990	94.00
1950-1959	125,489	13,711	90.15
1958-1960	43,530	7,276	85.68
New York			
(rest of state)			
1940-1949	57,204	8,436	87.15
1950-1959	77,224	16,852	82.09
1958-1960	22,361	7,141	75.79
New Jersey			
1900-1939	-----	-----	99.17
1940-1949	50,305	3,922	92.76
1950-1959	226,744	28,631	88.79
1958-1960	104,640	10,542	90.85
Pennsylvania			
1900-1939	-----	-----	95.39
1940-1949	63,933	9,953	86.52
1950-1959	90,307	55,738	61.83
1958-1960	20,456	21,043	49.29
Delaware			
1900-1939	-----	-----	99.08
1940-1949	21,777	634	97.17
1950-1959	118,489	85,175	58.18
1958-1960	31,288	42,432	42.44
Maryland			
1900-1939	-----	-----	94.08
1940-1949	23,309	3,108	88.23
1950-1959	102,184	60,343	62.87
1958-1960	43,482	30,719	58.60
Washington, D.C.			
1940-1949	1,854	376	83.14
1950-1959	7,619	2,170	77.83
1958-1960	1,717	449	79.27
Virginia			
1900-1939	-----	-----	67.53
1940-1949	15,557	2,599	85.67
1950-1959	68,736	31,259	68.74
1958-1960	26,531	13,706	65.94
North Carolina			
1900-1939	-----	-----	90.13
1940-1949	3,133	1,831	63.10
1950-1959	28,830	29,522	49.41
1958-1960	16,849	16,593	50.38

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
South Carolina			
1900-1939			71.35
1940-1949	3,232	1,534	67.84
1950-1959	3,169	49,281	6.04
1958-1960	1,483	32,341	4.59
Georgia			
1900-1939			70.58
1940-1949	21,266	10,882	66.10
1950-1959	169	2,258	6.96
1958-1960	210	984	17.59
Florida			
1900-1939			65.98
1940-1949	1,188	1,854	29.09
1950-1959	1,142	4,164	21.52
1958-1960	301	1,296	19.00
Ohio			
1900-1939			66.89
1940-1949	33,983	22,266	60.32
1950-1959	105,670	150,582	41.23
1958-1960	65,153	78,541	45.34
West Virginia			
1900-1939			88.01
1940-1949	622	35	94.67
1950-1959	1,321	674	66.21
1958-1960	642	427	60.06
Kentucky			
1900-1939			15.31
1940-1949	8,216	11,083	42.74
1950-1959	39,902	375,891	9.60
1958-1960	6,912	23,875	22.45
Tennessee			
1900-1939			19.54
1940-1949	4,477	33,844	11.68
1950-1959	6,044	354,969	1.67
1958-1960	8,288	176,772	4.48
Alabama			
1940-1949	4,257	19,380	18.02
1950-1959	5,024	59,720	7.70
1958-1960	89	380	18.98
Mississippi			
1900-1939			14.56
1940-1949	96	1,119	7.90
1950-1959	2	11,621	0.02
1958-1960	0	178	0.00

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
Michigan			
1900-1939	-----	-----	71.75
1940-1949	7,800	6,656	53.91
1950-1959	15,275	11,990	56.02
1958-1960	2,146	1,868	53.46
Indiana			
1900-1939	-----	-----	21.37
1940-1949	26,425	93,660	22.03
1950-1959	68,372	1,442,230	4.53
1958-1960	4,935	69,187	6.65
Illinois			
1900-1939	-----	-----	8.52
1940-1949	51,625	2,311,226	2.19
1950-1959	74,486	1,410,753	5.01
1958-1960	11,112	290,805	3.68
Wisconsin			
1900-1939	-----	-----	10.10
1940-1949	7,175	14,794	32.38
1950-1959	12,543	41,853	23.06
1958-1960	3,452	22,118	13.50
Minnesota			
1900-1939	-----	-----	0.07
1940-1949	36	3,337	1.07
1950-1959	682	8,705	7.26
1958-1960	31	4,463	0.69
Iowa			
1900-1939	-----	-----	0.22
1940-1949	65	29,745	0.22
1950-1959	210	45,724	0.46
1958-1960	207	13,949	1.46
Missouri			
1900-1939	-----	-----	0.70
1940-1949	460	94,516	0.48
1950-1959	163	275,485	0.06
1958-1960	93	168,045	0.06
Arkansas			
1900-1939	-----	-----	0.33
1940-1949	1	871	0.12
1950-1959	136	479,094	0.03
1958-1960	32	156,625	0.02
Louisiana			
1900-1939	-----	-----	7.57
1940-1949	490	20,626	2.33
1950-1959	194	28,228	0.68
1958-1960	54	4,581	1.16

TABLE I.—(continued)

State or Province	Total Black Ducks	Total Mallards	Per cent Black Duck
North Dakota			
1940-1949	1	1,977	0.05
1950-1959	0	1,661	0.00
1958-1960	0	99	0.00
South Dakota			
1900-1939	-----	-----	0.21
1940-1949	10	340,265	0.003
1950-1959	35	484,132	0.01
1958-1960	10	300,664	0.003
Nebraska			
1940-1949	0	475	0.00
1950-1959	0	119,635	0.00
1958-1960	0	226,468	0.00
Kansas			
1940-1949	13	18,457	0.07
1950-1959	23	278,104	0.01
1958-1960	4	58,712	0.007
Oklahoma			
1940-1949	65	271,791	0.02
1950-1959	42	219,765	0.02
1958-1960	5	34,058	0.01
Texas			
1900-1939	-----	-----	0.85
1940-1949	29	371,396	0.01
1950-1959	122	780,629	0.01
1958-1960	17	134,715	0.01

the eastern states as a breeding bird, but counts made by federal and state biologists during the breeding season indicate that Mallard-Black Duck ratios in the northern states and provinces during the period 1948-1956 closely parallel the wintering ratios of those areas for the same period (Johnsgard, 1959).

It would appear that the Mallard has in the past few decades made enormous inroads into what formerly was predominantly Black Duck territory, whereas the reverse is true only to a very limited extent in the Great Lakes region. Probably this can be attributed to the great changes in land use, and the deforestation, which have occurred in the East during the present century, and which have had the effect of decreasing Black Duck breeding habitat while at the same time increasing Mallard habitat. Whether sufficient preservation and regeneration of the northeastern forests will occur to permit the Black Duck to retain a stronghold is impossible to predict, but it appears likely that the Black Duck, through hybridization with the much larger

Mallard gene pool and through the constant reduction of its breeding habitat, may eventually disappear as a distinct entity from our fauna.

Acknowledgment.—This study was done at Cornell University under the support of fellowships from the Cornell University Graduate School and the National Science Foundation. I would like to express my appreciation to these agencies as well as to Dr. C. G. Sibley, my graduate committee chairman.

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The Effects of Fires in the Okefenokee Swamp in 1954 and 1955

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ABSTRACT: In 1954 and 1955 during an extended drought, serious fires occurred in the Okefenokee Swamp and on the adjacent upland. There was considerable destruction of pine timber on the upland and some damage to the cypress and blackgum forests within the swamp but the belief that the whole character of the swamp has been altered is erroneous.

Recurrent droughts and fires have long played an important part in the ecology of the swamp as is evidenced by charred stumps embedded in the peat and by charcoal deposits several feet below the surface.

Five major fires between July 1954 and June 1955 burned over about 318,000 acres of the swamp and 140,000 acres of adjacent upland. Most of the swamp was lightly or moderately burned. Severe burns were spotty. Coppice growth is rapidly replacing the timber which was killed in the more severely burned areas. The numbers of otters, raccoons, snakes and most fish were drastically reduced during the drought. Alligators, sandhill cranes, herons, waterfowl and bears were not adversely affected and some of these may have actually been favored.

INTRODUCTION

In 1954 and 1955, during an extended drought, fires occurred in the Okefenokee Swamp and surrounding upland in southeast Georgia and northeast Florida. The drought was so severe that the upper layer of the peaty floor of the swamp dried out and became flammable. The peat fires which ensued could not be controlled, with the result that the fire swept over about 80 per cent of the Swamp. Also, about 140,000 acres of pine forests surrounding the swamp were so severely burned that an almost complete kill of timber followed.

Because of the destruction in the large area of surrounding pine lands and because of severe burns in certain places within the Okefenokee Swamp, a misunderstanding about the effects of the fire on the character of the swamp has become prevalent. It has been generally believed that the fires have destroyed the swamp's cypress and blackgum forests, leaving charred desolation nearly void of life.

Actually, while some parts of the swamp were severely burned, most of the area reached by fires was only moderately or lightly burned and only temporary alteration, or none at all, resulted.

This paper is an attempt to appraise the effects of the drought and the fires on the ecology of the swamp.

DESCRIPTION OF THE SWAMP

Okefenokee Swamp covers approximately 412,000 acres in Ware, Charlton and Clinch counties, Georgia, and Baker County, Florida.

Approximately 321,725 acres of the swamp and 9,250 acres of adjacent upland are included in the Okefenokee National Wildlife Refuge.

The elevation above sea level ranges from about 130 feet on the northeast side to about 105 feet on the southwest side. The swamp's existence is due to Trail Ridge, a sand bar formed during the early Pleistocene period when the coast line was about 70 miles farther inland and the sea level was about 160 feet higher in relation to the land than at present. After the recession of the coast line, this ridge acted as a barrier to prevent the drainage of the shallow basin thus formed (MacNeil, 1940).

The principal outlet of the swamp is the Suwannee River which empties into the Gulf of Mexico. Some of the drainage is through the St. Mary's River which empties into the Atlantic Ocean.

Considering the size of the swamp, the watershed of the Okefenokee is small. Along the east and northeast sides the drainage area, which extends from the crest of Trail Ridge to the swamp edge, averages only about one mile in width. The sandy soil of Trail Ridge erodes very little and, consequently, deposits little silt into the swamp. On the north and northwest sides, about 300,000 acres drain into the swamp. This is flat, sandy land, with very little, if any, erosion. The almost complete absence of siltation accounts for the Okefenokee's persistence.

Except for a few small open water areas, the Okefenokee basin is filled with peat almost to the average water level. This peat deposit, which varies up to 20 feet or more in depth, serves as the floor of the swamp. About 85 per cent of the swamp is covered, more or less densely, with forests in which either pond cypress (*Taxodium distichum nutans*) or swamp blackgum (*Nyssa sylvatica biflora*) predominate. The principal secondary species are red bay (*Gordonia lasianthus*), white bay (*Magnolia virginiana*), sweet bay (*Persea borbonia*), red maple (*Acer rubrum*), cassena (*Ilex cassine*) and titi (*Cyrilla racemiflora*).

The forest understory is principally hurrah bush (*Desmodium lucidus*), titi, swamp fetterbush (*Leucothoe racemosa*), he-huckleberry (*Arsenococcus ligustrinus*), poor-man's soap (*Clethra alnifolia*), black bamboo (*Smilax laurifolia*), red bamboo (*Smilax walteri*), and sweet spire (*Itea virginica*).

The so-called "prairies," which are actually marsh and open water areas, cover the remainder of the swamp. These prairies contain a variety of herbaceous marsh and aquatic vegetation. White water lilies (*Nymphaea odorata*), spatterdock (*Nuphar advena*), beakrush (*Rhynchospora inundata*), neverwet (*Orontium aquaticum*), chain fern (*Woodwardia virginica*), paintroot (*Gyrotheca tinctoria*), maidencane (*Panicum hemitomon*), pipewort (*Ericaulon compressum*) and false maidencane (*Sacciolepis striata*) are prominent.

Scattered throughout the prairies are small clumps of trees and shrubs called "houses." These houses vary in size from only a few

burned out which were the cause of the majority of the lakes in there."

The Okefenokee prairies were caused by extremely hot fires which killed all plants, root systems included, and burned away the peat to a low enough level to prevent the re-establishment of woody vegetation. Charred stumps, embedded in the peat throughout the prairies, are evidence of extensive forests which were killed by fire.

Fires which resulted in prairie formation must have occurred during droughts which were much more extreme than any in recent years. Undoubtedly, the prairie lakes were the results of great pockets being burned out in the peat. There are at least 40 of these lakes large enough to be designated by names and innumerable small un-named "gator holes." The largest are Gannett Lake (28 acres), Coward Lake (22 acres) and Double Lakes (36 and 18 acres).

In order to learn whether the lakes exist because of the topography of the underlying sand floor of the swamp or because of the topography of the overlying peat, series of soundings were run across three of them: Buzzard Roost, Monkey and Cooter Lakes. In no case was there an indication of a relationship between the presence of the lake and the topography of the underlying sand floor. In other words, the lakes are holes in the peat, rather than holes in the underlying sand, which gives credence to the belief that the lakes were fire caused.

While the fire of 1844 may have been severe enough to have caused prairies and lakes, we know that there were extensive prairies in Okefenokee Swamp antecedent to that fire. General Charles Floyd, who entered the swamp with a company of men during the Seminole Wars in 1838, wrote of a large lake east of Floyd's Island (Hopkins, 1947). This "lake" must have been Chase Prairie. He also wrote of an extensive prairie west of Floyd's Island "level as a lake and covered with short grass and adorned with beautiful islands" (Walker and King, 1947). This area is known as Floyd's Prairie.

There is evidence that extremely severe fires occurred in the

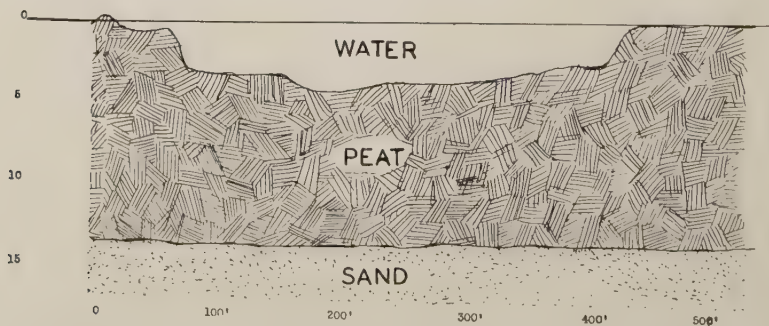


Fig. 2.—The topography of Monkey Lake indicating the relation between surface peat and sand floor.

Okefenokee much earlier than those which caused the present prairies. J. Gordon Erdman made a series of corings in the peat in Floyd's Prairie, Chase Prairie and near Minnie's Lake in 1957. Charcoal was found at depths of 5'3" and 5'9" in one coring and at 4'5", 6'7" and 7'3" in another. This last coring was made to a depth of 7'7" which was the deepest made by Dr. Erdman (correspondence).¹

Datings have not been made of these corings at this writing. Some idea of the rate of peat accumulation may be obtained from information submitted by Dr. Erdman on the datings of samples collected at a depth of 3'10" to 4'3" in Tamarack Swamp near Columbus, Pennsylvania and 3'7" to 3'11" in Graveline Bay, near Pascagoula, Mississippi. By C¹⁴ datings, the former was given an age of 2820 ± 250 years, the latter 2220 ± 180 years.

Since the Okefenokee corings indicate that the peat has been burned away to depths of several feet on several occasions and then redeposited, it can be assumed that the deeper charcoal deposits were the results of fires which occurred many thousands of years ago.

FIRES DURING THE 1954-1955 DROUGHT

During the period from January 1, 1954 to June 30, 1955, only 44.25 inches of rainfall were recorded at the Weather Bureau station at Camp Cornelia on the east side of Okefenokee Swamp. During the entire year 1954 there were only 26.07 inches of precipitation which is in sharp contrast to the average annual precipitation of 56.39 inches from 1939 to 1953.

The water level at Camp Cornelia fell to a low of 117.56 on November 14, 1954. This was 3.53 feet below the 1941-53 average water level at this station. By November 22, the water level at Billy's Lake had fallen to 110.44 feet, 3.92 feet below the 1941-53 average. The bed in the upper part of Billy's Lake went dry, as did much of Minnie's Lake and Big Water Lake. At this time there was very little surface water anywhere in the swamp.

During such extreme drought, the upper part of the swamp's peat bed dries out and the entire surface of the swamp's floor becomes tinder. If fire enters the swamp at such a time, there is no known way to control it.

Roy Moore (1955) described two types of swamp fire:

"One being the surface fire that often moves fast, burning combustible materials on and above the swamp floor, and including crown fires that flame through the tree tops. Surface fires usually succumb to a heavy shower of rain. The other type is the peat fire that burns below the surface in the organic soil and debris of the swamp floor. Peat fires may be started by lightning or by surface fires. They move slowly in an irregular patchwork pattern. Sometimes they

¹ These data furnished by J. G. Erdman, Mellon Institute, Multiple Fellowship on petrolcum sponsored by Gulf Research and Development Company.

go out for no apparent cause; and often they continue to burn through half a foot or more of rain, until with the return of dry windy weather, they may give rise to the fast moving surface fires. A peat fire destroys every living thing that can't get out of its way. The roots of a giant cypress are burned away as readily as those of a hurrah bush."

A fire sweeping across the swamp may gain such headway that control, when it reaches the upland, is extremely difficult.

Billy's Island Fire.—The first major fire of the 1954-1955 drought occurred on Billy's Island. This fire, which was probably caused by lightning, burned from July 6 to July 12, 1954 and swept over the whole of Billy's Island, which is about 3000 acres in size. Probably the peat was not dry enough at this time to burn. The fire did not extend beyond the limits of the island.

Very few trees were killed. The accumulation of litter burned fairly clean and this proved later to be the salvation of the timber on the island. When it burned over again the following March, the fire was not nearly as severe as it might have been had the July fire not occurred.

Mule-tail Fire.—The "Mule-tail Fire" began on November 27, 1954. It has been told that this fire was started by a mule which was being used by Negro laborers collecting turpentine gum in the pine woods just southeast of the refuge. It is said that the mule switched its tail into a barrel of turpentine gum, then switched it into a fire which the laborers were warming by, then, its tail a torch, raced through the woods, scattering fire as it went. The account is probably apocryphal but it is a good story and has been widely circulated. At any rate, the fire was started by turpentine collectors.

The first control efforts were made toward preventing the spread of the fire through the upland. The swamp was regarded as a fire break. But it was dry enough that the fire swept westward into the swamp and then northward on a five mile front. Re-emerging on the upland on the east side of the swamp near Chesser Island, the fire crowned in the pine woods causing an almost complete kill on 20,650 acres of timber. An estimated 33,350 acres of swamp burned over. The fire was brought to a stop by a shower the night of December 5.

The Big Fire.—The most extensive fire of the drought period had two separate origins. One, which was probably the result of lightning, was discovered October 6, 1954. This fire began on the west side of the swamp about one mile northeast of Rowell's Island. It burned slowly and smouldered along for the next five months.

The other fire, which was discovered March 5, 1955, was of incendiary origin. It resulted from the setting of several fires along a seven mile stretch between Turkey Branch and Suwannee Creek from one to three miles west of the refuge.

These two fires came together on or about March 9 and continued to burn and spread until May 14, when stopped by rain.

Approximately 318,000 acres of swamp burned over. About 11,100 acres of pine timber on the upland were destroyed before the fire was brought under control.

Besides burning over approximately 279,000 acres of swamp which had not previously been burned during the drought, this fire re-burned all of the 39,000 acres of swamp which had been burned in the other fires.

The State Forest Fire.—A fire of incendiary origin began near the north end of the swamp on Waycross State Forest March 6, 1955. This fire severely burned pine lands on the upland causing an almost complete kill of timber on about 22,500 acres. About 5,000 acres of swamp were burned over. It was brought under control March 14.

St. Regis Fire.—The most destructive fire of the drought was set by lightning at a point about nine miles northwest of Fargo, June 8, 1955, and spread rapidly eastward causing almost complete kill of pine timber on about 82,500 acres, mostly on lands of St. Regis Paper Company. This fire was brought under control at the swamp's edge near the Suwannee River and at about the limits of the March burn.

GENERAL EFFECTS OF THE FIRE ON THE ECOLOGY OF THE SWAMP

As stated above, the effect of the fires within the swamp was not as destructive nor as enduring as has been supposed by many who have seen only the severe destruction of the pine timber adjacent to the swamp. It was only where pockets of peat were burned out



Fig. 3.—Invasion of a severely burned spot near Soldier Camp Island by woody and herbaceous vegetation three years after the 1954-55 fires.

that the larger cypresses and blackgums were killed. These were encountered only occasionally. Where only surface fires occurred, the larger trees survived.

The fires in the cypress and blackgum bays burned with varying degrees of severity. In places there were pockets of peat burned out sometimes to a depth of two or three feet. Usually all trees were killed where peat burned to this depth. These pockets were usually less than 1/10 acre. Over most of the area the burns were surface fires which generally killed most of the reproduction and underbrush but rarely burned severely enough to kill the larger trees. In many places the fire swept over lightly, burning the surface duff and killing only the smaller underbrush. Some places were missed entirely. At no place was the fire intense enough to cause a complete kill of woody cover over as much as one acre.

The most severe burns occurred in places where timber operations had been conducted in past years, probably because the hottest fires occurred where low brushy growth was most dense, as in places where trees had been cut and skidded. Virgin cypress forest usually burned lightly and sustained little damage; virgin forest in which blackgum and bay were predominant usually burned lightly except that there were occasional severely burned small pockets.

In order to arrive at an estimate of the extent and damage in parts of the swamp where the damage was considered typical, two transects of 50 chains each were staked out. One of these extended from the upland at a point about one mile northeast of the north tip of Rowell's Island and ran eastward into the swamp (Fig. 1, A). The other extended from the Pocket near Jones Island westward and northward into the swamp (Fig. 1, B). Both of these transects were through typical blackgum bay.

All trees, both live and fire-killed, were tallied according to species for a 25-link width along these transects. Tables I and II

TABLE I.—Stem count and basal area per acre of live and fire-killed trees in Transect A

	Stem Count			Basal Area		
	Live	Dead	Total	Live	Dead	Total
<i>Taxodium distichum</i>	26	3	29	10.491	.096	10.587
<i>Nyssa sylvatica</i>	358	27	385	139.505	8.348	147.853
<i>Cyrilla racemiflora</i>	11	3	14	.693	.096	.789
<i>Magnolia virginiana</i>	125	6	131	23.253	2.456	25.709
<i>Gordonia lasianthus</i>	25	3	28	2.302	.035	2.337
<i>Persea borbonia</i>	9	0	9	.475	0	.475
<i>Cephalanthus occidentalis</i>	2	1	3	.074	.053	.127
<i>Ilex cassine</i>	222	20	242	6.516	.395	6.911
<i>Acer rubrum</i>	108	22	130	5.551	1.414	6.965
<i>Desmothamnus lucidus</i>	1	0	1	.018	0	.018
Grand Totals	887	85	972	188.839	12.910	201.749

show the stem count and the basal area per acre of the tallied trees by species.

As shown in these two tables the shrubby species, such as titi, hurrah bush and buttonbush sustained the greatest kill. The ratio of the live to the fire-killed trees in the basal area column shows that the larger trees were not killed to any great extent.

EFFECTS OF THE SEVERE BURNS

There is no known place in the swamp where the 1954-1955 fires burned severely enough over a large enough area to result in a prairie or lake. Coppice is rapidly restoring the forest that was killed in the more severely burned spots.

Usually severe burns were small and spotty but three such burns were fairly extensive: one in an area between Billy's Lake, Minnie's Island and Hickory Island; another north and west of Soldier Camp Island; and the third north of Suwannee Canal, between Camp Cornelia and Mizell Prairie. There were about 500 acres in each of these areas. Except for surviving roots, nearly all the trees in each were killed.

In order to have a record of the plant succession following the fire, sample one-acre plots were staked out in each of the severely burned areas (Fig. 1, C, D, E). Each plot was 10 chains long and one chain wide. All live and fire-killed trees as much as one inch in diameter at four and one-half feet above the ground were measured and recorded to indicate the composition of the forest prior to the kill. Probably some of the smaller trees were burned away and could not be measured.

Billy's Lake Burn.—The area north of Billy's Lake was covered by typical blackgum-bay forest. The peat depth in this plot averages about eight feet. The surface peat was burned away in spots as much as a foot or more.

TABLE II.—Stem count and basal area per acre of live and fire-killed trees in Transect B

	Stem Count			Basal Area		Total
	Live	Dead	Total	Live	Dead	
<i>Taxodium distichum</i>	8	2	10	5.432	.148	5.580
<i>Nyssa sylvatica</i>	234	70	304	95.846	7.525	103.371
<i>Pinus elliotii</i>	0	4	4	0	.160	.160
<i>Cyrilla racemiflora</i>	47	79	126	2.673	4.539	7.212
<i>Magnolia virginiana</i>	148	134	282	40.710	12.650	53.360
<i>Gordonia lasianthus</i>	28	31	59	3.252	4.877	8.129
<i>Persea borbonia</i>	50	54	104	7.530	8.022	15.552
<i>Cephalanthus occidentalis</i>	2	2	4	.074	.053	.127
<i>Ilex cassine</i>	12	2	14	.830	.196	1.026
<i>Acer rubrum</i>	18	38	56	3.170	4.187	7.357
<i>Desmodium lucidus</i>	3	50	53	.070	1.091	1.161
Grand Totals	550	466	1016	159.587	43.448	203.035



Fig. 4.—Recovery of woody growth three years after severe burning near Billy's Lake.

The composition of the resprouts is essentially the same as was the composition of the forest prior to the fire (Table III). The table does not reflect the true composition of the underbrush prior to the fire because much of this was burned away and could not be measured.

Suwannee Canal Burn.—Prior to 1932, the cover along the north side of the Suwannee Canal had been predominantly pond cypress and slash pine. Most of the timber was killed by fire during the 1932 drought. By 1954 the area had regrown in a dense thicket of pond cypress, bay, hurrah bush, titi and bamboo vine. The Mule Tail fire of November, 1954, followed by the fire of March, 1955,

TABLE III.—The number of stems, basal area, and sprouts of trees and shrubs in Billy's Lake plot

	Number of Stems		Basal Area		Sprouts
	Live	Fire-killed	Live	Fire-killed	
<i>Taxodium distichum</i>	0	8	0	.675	1
<i>Gordonia lasianthus</i>	0	430	0	65.524	56
<i>Ilex cassine</i>	0	37	0	2.773	13
<i>Magnolia virginiana</i>	0	137	0	13.922	36
<i>Cyrilla racemiflora</i>	0	125	0	5.846	39
<i>Desmodium lucidus</i>	5	5	0	.030	4
<i>Nyssa sylvatica</i>	0	135	0	39.421	38
<i>Persea borbonia</i>	0	7	0	1.085	14
<i>Acer rubrum</i>	0	10	0	.986	3
<i>Clethra alnifolia</i>	0	0	0	0	2
<i>Itea virginica</i>	0	0	0	0	23

burned away this brush and killed the few surviving large trees. The peat here was about six feet thick. About one foot of this burned away.

By 1958 woody growth was re-established sparsely (Table IV). The recovery here is less evident than in the burns at Billy's Lake or Soldier Camp Island, probably because this area had been severely burned in 1932 and then reburned in the recent fires. Possibly another such fire here would result in prairie.

Soldier Camp Island.—Prior to the fires, the forest on this area was predominantly pond cypress. The Mule Tail fire of November, 1954, killed or severely burned much of the timber and underbrush. By the time the fire of 1955 swept through, this dead underbrush had dried to the extent that it was much more flammable, and the intensity of the burning was such that nearly all surviving trees were killed.

The peat was shallower than average in this particular area; usually less than two feet in depth. This peat bed was entirely consumed. However, since the peat was shallow, the roots of most of the trees and shrubs reached the underlying sand and were partially protected. Root survival was such as to result in a substantial regrowth as shown in Table V.

PLANT SUCCESSION IN THE SEVERELY BURNED AREAS

All ground cover in both the Suwannee Canal plot and the Soldier Camp Island plot was mapped in 1956. The Suwannee Canal plot was remapped in 1957 and again in 1958. The Soldier Camp Island plot was remapped in 1958. Usually the cover was mapped and recorded according to species. In those cases where the cover was a mixture of two or more species, it was mapped as an association and the percentage of each species was estimated. The submerged

TABLE IV.—The number of stems, basal area and sprouts since the fires of trees and shrubs in Suwannee Canal plot

	Number of Stems		Basal Area		Sprouts
	Live	Fire-killed	Live	Fire-killed	
<i>Taxodium distichum</i>	1	29	1.396	3.993	14
<i>Pinus elliottii</i>	0	8	0	4.855	1
<i>Magnolia virginiana</i>	0	43	0	.880	18
<i>Ilex glabra</i>	0	4	0	.056	11
<i>Gordonia lasianthus</i>	0	19	0	1.416	0
<i>Persea borbonia</i>	0	29	0	.575	18
<i>Ilex cassine</i>	0	3	0	.093	0
<i>Nyssa sylvatica</i>	0	1	0	.006	5
<i>Leucothoe racemosa</i>	0	0	0	0	12
<i>Itea virginica</i>	0	0	0	0	76
<i>Vaccinium arkansanum</i>	0	0	0	0	2
<i>Desmodium lucidus</i>	0	0	0	0	35
<i>Arsenococcus ligustrinus</i>	0	0	0	0	1

TABLE V.—The number of stems, basal area and sprouts since the fires of trees and shrubs in Soldier Camp Island plot

	Number of Stems		Basal Area		Sprouts
	Live	Fire-killed	Live	Fire-killed	
<i>Pinus elliottii</i>	0	793	0	28.960	2
<i>Taxodium distichum</i>	4	650	2.650	59.854	53
<i>Myrica cerifera</i>	0	0	0	0	1
<i>Magnolia virginiana</i>	0	49	0	.711	12
<i>Persea borbonia</i>	0	27	0	.296	74
<i>Ilex glabra</i>	0	0	0	0	4
<i>Ilex coriacea</i>	0	0	0	0	1
<i>Gordonia lasianthus</i>	0	22	0	.389	2
<i>Nyssa sylvatica</i>	0	283	0	4.391	20
<i>Clethra alnifolia</i>	0	0	0	0	32
<i>Desmodium lucidus</i>	0	0	0	0	33
<i>Arsenococcus ligustrinus</i>	0	0	0	0	1
<i>Itea virginica</i>	0	0	0	0	1

aquatic plants, sphagnum and bladderwort, which occupied nearly all of the area not occupied by other plants, were not recorded. Tables VI and VII show the percentage of ground cover by species as mapped in these plots.

The year after the fire, herbaceous growth on the Soldier Camp Island plot was predominantly paintroot and beakrush. By 1958



Fig. 5.—Sparse recovery of woody growth in repeatedly burned area near Suwannee Canal. This would probably become prairie with one more severe burn.

this cover had been largely replaced by a variety of other herbaceous plants, a sedge, hardhead, fern and bur marigold being the predominating species.

By 1957, paintroot had invaded a considerable part of the Suwannee Canal plot. In 1958 this plant was replaced largely by

TABLE VI.—Soldier Camp Island plots showing per cent coverages in 1956 and 1958

<i>Trees and Shrubs</i>	1956	1958
<i>Pinus elliotii</i>	0	t
<i>Taxodium distichum</i>	.03	.37
<i>Smilax laurifolia</i>	.01	.08
<i>Smilax walteri</i>	0	t
<i>Myrica cerifera</i>	0	t
<i>Magnolia virginiana</i>	.01	.12
<i>Persea borbonia</i>	.05	.41
<i>Ilex glabra</i>	.01	.03
<i>Ilex coriacea</i>	0	t
<i>Gordonia lasianthus</i>	0	.01
<i>Nyssa sylvatica</i>	.01	.59
<i>Clethra alnifolia</i>	0	.16
<i>Desmodium lucidus</i>	0	.20
<i>Vaccinium arkansanum</i>	0	t
<i>Itea virginica</i>	0	t
<i>Herbs</i>		
<i>Woodwardia virginiana</i>	*	10.93
<i>Sagittaria graminea</i>		1.53
<i>Andropogon sp.</i>		t
<i>Panicum sp.</i>	.05	.33
Unidentified grasses		.11
<i>Rhynchospora fascicularis</i>	**	.77
Unidentified sedge	.09	8.69
<i>Xyris sp.</i>		5.92
<i>Pontederia cordata</i>	.06	.50
<i>Gyrotheca tinctoria</i>	50.79**	7.33
<i>Hypericum spp.</i>		1.54
<i>Hypericum virginicum</i>		.78
<i>Ludwigia lanceolata</i>		.79
<i>Rhexia virginica</i>		.77
Mint		.79
<i>Bidens coronata</i>		2.89
<i>Eupatorium capillifolium</i>		.78
<i>Pluchea foetida</i>		.77
<i>Solidago fistulosa</i>		t

* In 1956 there was a fringe of ferns at the base of most trees and stumps, the amount of which was not estimated.

** In 1956 this cover included a mixture of *Rhynchospora fascicularis* which had almost disappeared in 1958.

fern and sedge. Hardhead, which was a predominant species in 1956, had nearly disappeared by 1958. Just as in the Soldier Camp Island plot, sedge had steadily increased.

Of the species recorded in these plots, paintroot is of considerable value as a food for sandhill cranes and ducks. Apparently this plant was temporarily favored by the burn but it is rapidly being replaced by less desirable species. Bur marigold, a fair duck food plant, had increased on both areas by 1958.

As would be expected, coppice growth of the woody species has increased steadily since the fire.

EFFECTS ON ANIMAL LIFE

The effects of the drought and fires of 1954-55 on animal life of the Okefenokee Swamp have been varied. Some forms, notably fish and some animals directly dependent upon fish, were adversely affected. Other forms were not appreciably affected, or were actually favored.

Fish.—Okefenokee Swamp has long been famous for its sport fishing. The principal species taken are largemouth bass (*Micropterus salmoides*), bluegill sunfish, (*Lepomis macrochirus*), warmouth sunfish (*Chaenobryttus coronarius*), flyers (*Centrarchus macropterus*) and pickerels (*Esox niger*). Catfish (*Ictalurus nebulosus*) and mudfish (*Amia calva*) are also commonly taken.

TABLE VII.—Suwannee Canal plot showing per cent of ground cover by species in 1956, 1957 and 1958

<i>Trees and Shrubs</i>	1956	1957	1958
<i>Pinus elliottii</i>	0	0	t
<i>Taxodium distichum</i>	0	.24	.23
<i>Magnolia virginiana</i>	.05	.35	.90
<i>Persea borbonia</i>	.05	.30	.54
<i>Nyssa sylvatica</i>	0	.04	.05
<i>Smilax laurifolia</i>	.15	.17	.20
<i>Itea virginica</i>	.07	.44	.75
<i>Desmodium lucidus</i>	.34	.75	.63
<i>Leucothoe racemosa</i>	.01	.06	.24
<i>Arsenococcus ligustrinus</i>	0	0	t
<i>Vaccinium arkansanum</i>	0	.02	.01
<i>Ilex glabra</i>	.01	.08	.09
<i>Herbs</i>			
<i>Woodwardia virginica</i>	3.83	9.57	9.82
<i>Carex</i> sp.	16.25	46.07	52.46
<i>Dulichium arundinaceum</i>	.07	.43	t
<i>Andropogon</i> sp.	0	0	t
<i>Gyrotheca tinctoria</i>	0	9.57	.03
<i>Peltandra virginica</i>	.01	.01	.03
<i>Xyris</i> sp.	21.07	1.86	.51
<i>Ludwigia lanceolata</i>	1.28	18.25	0
<i>Bidens coronata</i>	0	0	.53

By November, 1954, the water level in the swamp was the lowest on record. The gauge reading at Camp Cornelia was 117.56 and at Billy's Lake it was 110.44. This was about four feet below normal, which means that most of the lakes and 'gator holes were dry or nearly dry. Naturally, fish concentrated at the few remaining places where there was water, as did also fish predators. The numbers of fish were sharply reduced. With the return of higher water levels, the decimated fish population was dispersed.

While the drought ended in the summer of 1955, the water levels remained comparatively low until June, 1957. Except for brief rises in March and May, 1956, the gauge readings at Camp Cornelia usually remained below 120.5 feet and the readings at Billy's Lake below 114 feet. When the water in Okefenokee remains at this low level, the acidity is high. pH readings were usually well below 4.5. Most fish do not reproduce readily in water as acid as this (Spector, 1956:457). It was not until April, 1957, that there was enough rain to raise the swamp water level to normal and to modify acidity enough to permit fish reproduction.

There was virtually no fishing in 1955. Since then, sport fishing has improved steadily. Catches in 1958 were reported to be the best in more than ten years.

Frogs.—If the frog population was reduced by the drought, it was not evident the following year. The cricket frog (*Acris gryllus*) is the most abundant vertebrate animal in the Okefenokee Swamp. These frogs are distributed throughout the area. Doubtless they are an important item of food for the Okefenokee wading birds.

The pig frog (*Rana grylio*), bronze frog (*Rana clamitans*), leopard frog (*Rana pipiens*) and the green tree frog (*Hyla cinerea*) are also numerous in the swamp. The squirrel tree frog (*Hyla squirella*), the grass frog (*Hyla ocularis*) and the pine woods tree frog (*Hyla femoralis*) are common on the swamp edge and on the islands.

Snakes.—While the abundance of cotton-mouth moccasins (*Agkistrodon piscivorus*) in the Okefenokee Swamp has been grossly exaggerated in popular literature, it is true that this species is the swamp's most common snake. Apparently the drought affected cotton-mouths adversely, as they were rarely seen the year afterward. When the swamp dried out, these snakes concentrated at the few places where there was open water, where they fell victims to predators. By 1958, cotton-mouths were seen oftener than in any year since the drought and it seems likely that their numbers are approaching those of the pre-drought population.

Alligators.—It does not appear that the alligator (*Alligator mississippiensis*) population was reduced by the drought and the fires. Probably they actually thrived on conditions brought about by the drought. These reptiles concentrated at the few remaining open water areas as did their prey — fish, turtles, otters, raccoons and birds.

There are no pre-drought figures on alligator populations but residents of the swamp area do not believe that the number of alligators was reduced by the drought. On a trip along the fifteen-mile water course between Camp Stephen Foster and upper Big Water, on a warm day in time of low water, a careful observer can often count as many as 4 alligators per mile. As many as 91 were counted along this course in a one-way trip October 23, 1958. They may be seen at about the same frequency along the Suwannee Canal. Forty-eight were observed along seven miles of this canal, November 20, 1958.

Otters.—There is no practical way of censusing these animals (*Lutra canadensis*) in the Okefenokee. However, we do know that the swamp's otter population was drastically reduced during the drought. Before the drought these mammals were commonly reported. Since the drought, they have been rare. During the years 1957 and 1958, only 14 of them were reported by refuge personnel, who spent not less than 100 man-days on patrols along refuge water courses on the alert for wildlife.

It is believed that the alligator was a major cause of the reduction in the number of otters. During the drought, otters concentrated at the few places in the swamp where there were water and concentrations of fish, with the result that they became easy victims of the alligators.

Raccoons.—Prior to the drought, the raccoon (*Procyon lotor*) was the most abundant large mammal in the Okefenokee Swamp. Like the otter, and probably for the same reasons, its numbers were drastically reduced during the drought. By the fall of 1958, the raccoon population had recovered and this animal is again abundant.

Bears.—The Florida black bear (*Euarctos floridanus*) was not numerous before the drought nor has it been since. According to refuge personnel and other residents in the vicinity of the swamp, there is no noticeable difference in their numbers just prior to or since the drought. There were 14 bears reported killed on the west side of the swamp in 1957 and 11 reported killed in the same area the following year. This is comparable to the estimates of kills before the drought. Fleetwood (1947) reported the following kills on the west side of the swamp from 1941 to 1946: 1941, 6; 1942, 10; 1943, 9; 1944, 4; 1945, 1; 1946, 19. Francis Harper (1927) estimated that an average of about twelve bears were killed annually.

Sandhill cranes.—There is no evidence that the sandhill crane (*Grus canadensis*) population in the Okefenokee was reduced by the drought or the fire. On the contrary, conditions since the drought appear to have been favorable to this bird. Crane counts made before and after the drought indicate that the resident population is about the same as it was before the drought and that the winter population is much greater.

In 1921, Francis Harper estimated that the sandhill crane population of Okefenokee was about 100 (Walkinshaw, 1949). Thomas and James Roddenberry counted 94 cranes in Chase Prairie from January 24 to 27, 1935 (Hebard, 1941). During a day spent in Chesser and Chase prairies in 1945, Dr. Walkinshaw and Ben Chesser counted 26 cranes. Raymond J. Fleetwood estimated that the swamp crane population was about 300 during the winter of 1947 and 1948. In ten trips into Chesser and Grand prairies that winter, his counts varied from 20 to 71.

These counts appear low when compared with recent counts.

On January 29, 1957, Dock A. Rider and I counted 522 in Chesser Prairie alone. During the winter of 1956-1957 in any day spent in Chesser and Grand prairies, an observer could see 100 or more cranes. It was estimated that the swamp's population was about 1000. The increase of paintroot, a favorite crane food, may have attracted this unusually large concentration of winter visitors. It is also likely that the normal winter population was augmented by migrants which ordinarily would have wintered in the Florida prairies which were dry at that time.

Water levels during the winter of 1957-58 were about normal. The crane population of that winter, while considerably below that of the previous winter, appears to have been higher than that of the winters prior to the drought. In five trips made during that winter from November to February across Chesser and Grand prairies, counts varied from 39 to 79 cranes. On December 20, 1958, Raymond Johnson and I counted 191 during a whole day spent in Chesser Prairie.

Hérons.—The common egret (*Casmerodius albus*) is the most abundant heron in the Okefenokee Swamp. Its numbers in different parts of the swamp vary with the seasons and with changing water levels so that comparisons of estimates before and after the drought do not make a very reliable basis for evaluating the effects of the drought and the fires on this species. Apparently its population has been affected little.

Fleetwood reported from 32 to 206 in trips across Chesser Prairie in 1947 and 1948. Carter reported an average of 25.0 observed in May, 1942 and 12.7 in June and July, 1942. These compare with observations made since the drought when six counts made in Chesser and Grand prairies through May, June and July in 1957 and 1958 averaged 25.5 individuals per trip. Ten trips made from September to December, 1957 and 1958 averaged 79.2 individuals per trip.

Two common egret rookeries, one near Chesser Island and one near the northern part of the swamp, which were thriving prior to the drought, have been non-existent since. However, there may be active rookeries in remote parts of the swamp which have never been found. One rookery at Steedley Bay, three miles northeast of

Fargo, which has been active for many years, had about 200 nests in 1958. There is no reliable estimate of the size of the rookery in past years.

There is no evidence that the population of great blue herons (*Ardea herodias*) has been changed as a result of the drought or fire. Out of 37 trips made into Chesser and Grand prairies during 1957 and 1958, an average of 1.8 herons per mile was observed. A few are always seen but they are never very numerous. Observations ranged from 0.1 to 6.1 herons per mile.

This compares with Carter's (1940) estimate of from 2 to 20 observed on a usual trip in the prairies. His trips probably covered from six to ten miles. Fleetwood reported that eight individuals were the most observed by him on any one trip into the swamp in the fall of 1947.

The green heron (*Butorides virescens*) population at Okefenokee apparently varies annually. Carter's reports of 1940 indicate that they were not particularly numerous that year but in the spring of 1942 there were 29 nests along Suwannee Canal at Camp Cornelia. During the years 1956, 1957 and 1958 these birds were fairly common, but not numerous, along Suwannee Canal. Judging from reports, the heron is certainly much less numerous than it was in 1942, but there is not sufficient evidence to indicate whether these numbers were affected by the drought or fires.

Ibises.—Wood ibises (*Mycteria americana*) are regular summer and fall visitors at Okefenokee. There is no evidence that the fires have resulted in more or less favorable conditions for them. Apparently the population varies with the water levels of the swamp. When water levels are low so that the prairies are only partially flooded, wood ibises become numerous in the fall, probably because they are attracted to the swamp by more readily available food. In the fall of 1956, the water levels were low and wood ibises were common. The following year water levels in the swamp were near normal and only a few were observed. In the fall of 1958, water levels were again low and wood ibises were again quite common.

The white ibis (*Eudocimus albus*) is an uncommon summer resident and, in years of low water, an abundant fall and early winter resident. During the fall of 1958, usually from 50 to 100 white ibises would be seen on a trip across Chesser and Grand prairies or on a trip to Big Water. On December 20, 1958, 522 ibises were reported in Chesser, Mizell and Chase prairies. This compares with Fleetwood's reports of several flocks ranging from 25 to 175 individuals during the spring of 1947. In 1948, from January through April, a time of unusually high water levels, Fleetwood reported four observations, ranging from four to fifty white ibises.

Waterfowl.—The prairies are the favorite feeding ground in the swamp for ducks. The 1954-55 fires, which burned over these areas only lightly, had no enduring effect.

Favorite waterfowl plants such as paintroot and smartweed intruded into the more severely burned places in the bays and houses but the area of such burns was so small that there has been no appreciable difference in waterfowl use.

The wood duck (*Aix sponsa*) is the only duck which is a permanent resident of the Okefenokee. During the spring and summer some four or five pairs are usually seen in a day spent in the swamp. In the fall and winter, over a hundred may commonly be seen during a day spent in the prairies. This is comparable to counts made by Fleetwood in 1947 and 1948 and by Carter in 1942.

The most numerous duck at Okefenokee during the fall and winter is the mallard (*Anas platyrhynchos*). An unusual observation was made by Jewett Hall and W. C. Cone who estimated about 2400 in Floyd's Prairie, on January 14, 1958. Ordinarily, several hundred will be seen in a day spent in Chesser, Grand, Mizell, Chase or Floyd's Prairie. They are usually to be seen in flocks of less than a hundred but they are sometimes more numerous. This compares with Fleetwood's reports of small flocks ranging up to 186 individuals through January and February, 1948. He reported a total of 571 seen January 9, 1948 in Chesser, Grand, Hog Island, Buck Lake, Chase, Floyd's and Sapling prairies by four parties. Carter reported that counts ranged from 100 to 500 in January and February, 1941.

Other ducks commonly observed in small numbers are the black duck, pintail, American widgeon, green-winged teal, shoveler, blue-winged teal, ringneck, lesser scaup, and bufflehead. These are the same species commonly seen before the 1954-55 drought and fires.

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Notes and Discussion

An Interesting Growth Relationship Between Two Specimens of *Erythrina sandwicensis*

A remarkable growth relation between two wiliwili trees (*Erythrina sandwicensis* Degener) was observed on Haleakala Mountain, Island of Maui, Hawaii. The trees which are endemic to the Hawaiian Islands occur in this area in two color phases, bright orange and pale yellow. While collecting seed from one of these groups of trees I observed what appeared at first glance to be a yellow-flowered branch rising from an otherwise red-flowering tree. Examination showed that a lower limb of the yellow flowering tree had at some time previous, grown between two branches of the red-flower tree so that the limb rested in its crotch. Subsequent growth in diameter of the two trees had caused the limb of the yellow-flowered tree to become totally encased in the crotch of the red-flowered tree.

In spite of the total encasement, both trees were still growing and apparently quite healthy. Specimens were not taken as it would be of interest to see what would be the ultimate fate of these trees.

In view of the large amount of tissue of the red-flowered tree, and the vigor of the yellow-flowered branch passing through it, it is of interest to ask whether a natural graft was formed between the two trees. The situation is remarkable since, by chance, two trees of one species, each with different colored flowers were involved.—E. J. BRITTEN, Associate Agronomist, Hawaii Agricultural Experiment Station.

Book Reviews

MAMMALS OF WISCONSIN. By Hartley H. T. Jackson. The University of Wisconsin Press, Madison. 1961. xxii + 504 p. \$12.00.

Many hours of field and laboratory investigations have culminated in this study of Wisconsin's mammalian fauna. Although organized in the form of a typical state list, this book goes beyond the "ordinary" in the scope of its coverage. The detailed treatment of the individual species with respect to: identification, habits, habitat and status is a welcome review of the literature of the Wisconsin taxa through 1959. Cogent observations, accumulated through the author's long field experience, are interestingly incorporated throughout. The book is profusely illustrated with excellent photographs and diagrams depicting pertinent identification characters and natural history observations from various sources.

It is difficult to find much in this book with which one might take issue. However, a few points might be mentioned. There is an inconsistency of usage with regard to the abbreviation of the word "premolar" in the dental formulae; in the introduction PM is used, whereas in most of the text the standard P, is used. Despite the wealth of illustrations mentioned before, there might have been more palatal views of teeth, to acquaint the novice with many of the standard characteristics used in identification.

Of particular interest to this reviewer is Dr. Jackson's division of the state into three "life zones" based on mammalian distributions: Canadian in the northern one-third; the Upper Austral extending from the southeastern corner by a narrow spit across the state and up the western side paralleling the Mississippi River; and the remainder, the Transition. In the Introduction these zones are typified by certain plant and animal species; in some cases, plant forms of questionable value as "characteristic" organisms have been used. For example, balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*) are used as characteristic of all of the Canadian zone when in actuality these are characteristic dominants of only a small section of Boreal forests in the extreme northwestern part of the state; also the use of hackberry, *Celtis occidentalis*, and pecan, *Carya illinoensis*, as characteristics for his Upper Austral zone is tenuous when both are rather uncommon in this region, the latter at best just reaching the state.

This is not the place for a full discussion of biogeography, but it might have been ecologically more meaningful to consider the relations of the mammalian distributions to those of the plants as presented by J. T. Curtis in his recent book, *The Vegetation of Wisconsin*. A cursory glance at the mammal distribution maps indicates the possibility of a "tension zone," quite comparable to that presented for plants by Curtis. Also, interpretations of the mammal distributions based on only the three broad zones, obscures any consideration of factors such as the prairie influence in the southwestern corner of the state.

These are only minor points, and in no way detract from the value of this handsome book. It is a comprehensive and lucid presentation of the mammalian fauna of this most interesting transition state. Dr. Jackson has not merely collated the available knowledge of these mammals, but has digested this information and presented it in a usable form. This book will be ranked among the outstanding state lists and hailed as a compendium of mammalian natural history.

Mammals of Wisconsin is recommended, without reservation, for any student of Wisconsin natural history and for all people, whether amateur or professional, who are interested in mammals.—JAMES A. MACMAHON, Department of Biology, University of Notre Dame, Notre Dame, Indiana.

THE PLANT COMMUNITY. By Herbert C. Hanson and Ethan D. Churchill. Reinhold Publishing Corporation, New York. 1961. 218 p. Illus. \$4.95.

The authors state in the preface that they, "have adopted as the central theme of this book the formation and nature of the plant community." This is a formidable undertaking as the nature of the community is certainly one of the most complex of ecological problems. The concept of communal relations among organisms and their relations to the environment is fundamental to ecology and an adequate understanding of community concepts is essential to any view of ecology. The authors' predilections as to the nature of the plant community and the means by which it may be described, analyzed and synthesized into a comprehensive and comprehensible intellectual structure are of particular importance in view of their choice of theme.

The book is divided into four parts: 1. Species and populations, two chapters on ecological characteristics of species and the grouping of species; 2. The community, two chapters on analytic and synthetic characteristics used in describing the community; 3. The dynamics of communities, one chapter; 4. Classification of communities, one chapter.

The first part of the book offers an excellent discussion of the ecological amplitude of species and emphasizes the genetic basis of species behavior. It is replete with examples from the literature and the authors' own work. It is noticeable here that the coverage is heavily weighted towards grassland. This continues throughout, as suggested by the following rough count of generic citations in the index: *Abies* 2, *Acer* 3, *Agropyron* 41, *Andropogon* 21, *Betula* 4, *Bouteloua* 36, *Bromus* 21, *Picea*, 4, *Pinus* 21, *Poa* 15, *Quercus* 15, *Stipa* 25. The requirements and competitive ability of species and the role of these in community organization are clearly and effectively handled.

The second part considers quantitative and qualitative methods of analysis and synthesis of communities. In general these are well stated and illustrated with appropriate examples although several usages seem inappropriate. Indices of similarity, such as that of Sorenson, should not be equated with measures of interspecific association. Such an index is more appropriately regarded as a synthetic characteristic since it commonly is used to compare two samples of vegetation or to construct a matrix among several samples. Even if used to compare samples within a single stand it does not serve as a measure of interspecific association as is suggested.

The introduction of the concept of density-dependent and density-independent factors as used by the animal ecologist seems to offer little advantage to the study of plant communities. The validity of the concept is in dispute among animal ecologists and its meaning is not clear. For example, in the present volume a density-independent factor is defined as "... one that has little or no effect on density (for example the CO₂ content of the atmosphere), because it rarely if ever influences the number of plants in an area." Another recent ecology textbook, Odum's "Fundamentals of Ecology" states (p. 209), density-independent aspects of the environment tend to bring about variations, sometimes drastic, in population density. . . ." Obviously the term is used in different ways which indicates the need for clarification and agreement among ecologists as to its meaning and validity. This confusion reflects the disparity of views existing among animal ecologists and plant ecology has no need of additional confusing terms.

The use of Raunkiaer's "normal" curve of frequency as an indication of uniformity or homogeneity has been the subject of much discussion in the past and, in the light of numerous criticisms of such use, it is surprising to find it suggested here as a test of uniformity within a stand and of homogeneity in

a community type. The very brief discussion of the species-area curve does not serve to make the concept clear to a novice ecologist nor does the simplified coverage allow the necessary qualifications. No citations to the relevant literature are given.

It is unfortunate that some of the problems of ecological terminology persist although this certainly cannot be laid to the authors of the present volume. Abundance, is used by them as synonymous with population density (number of individuals) while Cain and Castro in the recent "Manual of Vegetation Analysis" restrict its meaning to estimated numbers or the less frequently used average number of individuals per quadrat of occurrence.

Part three considers community dynamics including relation of communities to environmental gradients and habitat patterns, successional changes and non-directional changes in community composition. The authors adopt a view of climax as consisting of a pattern or mosaic of vegetation distributed on an environmental gradient.

The authors' views on the nature and classification of communities which are explicitly covered in part 4, but appear implicitly throughout, lean heavily upon the precepts of various European phytosociologists. A statement in the conclusion summarizes these views concisely. "Classification, however, when analytic data on intrinsic properties and descriptions are available, may begin with the basic units, which are usually small in area and homogeneous." The assumption that vegetation consists of small or large, homogeneous, basic units which can be identified and classified is one of the classical views of plant ecology and has many distinguished adherents. The authors are eminently justified in adopting and propounding these concepts. However, they do their prospective audience an injustice in that alternative views are given short shrift, and data supporting them is unrepresented or under represented. Gleason's "Individualistic Hypothesis" is dismissed, on page 67, as impossible but no adequate consideration is given here, or at any other point, to a decade of work in Wisconsin summarized by Curtis as "... conclusive proof of Gleason's individualistic hypothesis of community organization. . . ." Nor is the work of Whittaker, or Goodall which buttresses Gleason's hypothesis, cited in this context although, it is referred to in other circumstances. The not inconsiderable European literature paralleling Gleason's views is ignored.

The extensive work of the past ten years relating to ecological gradients is similarly dismissed, "The ecological gradients of importance to vegetation are unknown at the beginning of an investigation of the vegetation of an area and cannot be guessed before hand, so the ordination of communities according to ecological gradients is very difficult. There appears to be general agreement that the basis for securing understanding of nature must be the study of directly observable characters, and not hypothetical inferences about the relations between vegetation and environment." The establishment of meaningful gradients or orders is by no means so difficult, as evidenced in the work of Curtis, Bray, Goodall or Whittaker, none of which is cited in this context.

However, on page 172, the existence of gradients is attested, species composition gradually changing in response to decrease in soil moisture. The cline is segregated into units quantitatively on the basis of arbitrarily chosen values of cover and frequency for selected pairs of species. It is at least as likely that a meaningful ordination could be constructed and the cline then subdivided secondarily. The establishment of units initially, simply obscures the cline or gradient and valuable information concerning species behavior and changes in community composition may be lost.

In short, the case for a well defined series of community types is presented

without adequate attention to controversial viewpoints. Controversial viewpoints, as Egler noted a number of years ago, being "what the other fellow thinks: fundamental real basic facts are what the writer knows are true." It is interesting to note that the traditional problem of how similar "similar" (p. 71, 174) communities must be in order to be recognized as members of a community type is not adequately elucidated at any point. The example cited in chart 2 (p. 19) seems to represent a completely subjective segregation of community types and from the data offered could be readily divided into several other sets of communities or interpreted as a continuum. Certainly in itself it lends no conviction to the authors' thesis.

It is perfectly true, as the authors suggest that accepting the view of vegetation as varying continuously does not preclude the possibility of recognizing community types on the basis of arbitrary criteria if this is desirable. However, it should be clear what these criteria are. To attest to the utility of such classification by an analogy of the segregation between youth and old age can only leave those of us who range in the middle aged class to wonder how recently we left youth or how soon we arrive at old age, or whether to use chronology or "you're as old as you feel" as a yardstick.

The text is in general clear and few errors were noted, although occasional statements give some difficulty, viz.: "The independence of a species may be greatly modified when it is growing in association with other species as compared to growing alone." (p. 59.)

"In some cases it is a continuum, in others a series of communities, or it may be a continuum in one period, a distinct community in another. In most cases elements of both are present in varying proportions." (p. 69.)

"The environment is a controlling influence, not a property of vegetation and the successional status is often hypothetical, though important." (p. 173.)

The book is illustrated with well selected photographs largely from the files of the U.S.D.A. Numerous references to the British and Scandinavian ecological literature are given.

The Plant Community is designed for a one semester course in plant ecology, a supplement to textbooks in general ecology, as an adjunct to courses in various related subjects or for the general reader. Its use as a supplement to other texts, or selected readings is quite feasible. As a single volume text its utility is limited by the brevity of its coverage of difficult aspects of community analysis and synthesis and by an inadequate evaluation of current views of the nature of the community.—ROBERT P. MCINTOSH, University of Notre Dame, Notre Dame, Indiana.

THE USE OF CHEMICALS IN SOUTHERN FORESTS. Edited by Robert W. McDermid. Louisiana State University Press, Baton Rouge. 1961. v + 152 p. Illus. \$4.00.

This volume contains the published proceedings of the Ninth Annual Forestry Symposium held at Louisiana State University. It is composed of three parts: "Forest Fertilization," "Using Chemical Herbicides in Southern Forests" and "Chemical Use in Forest Protection."

Forest fertilization is fresh pasture in American forestry and its denizens are characteristically enthused about its provident potentialities. This is both admirable and dangerous. It is demonstrable that trees respond to artificially applied mineral amendments and that the nature of such response, in certain cases and under conditions of severe nutrient deficiency, is often striking. Such phenomena warrant investigation. The deficiencies in our knowledge concern-

ing the duration of such response, the effect of mineral amendments on wood quality and quantity, competitive growth and pathogenic susceptibility are equally impressive and deserve to be remembered. At an even more fundamental level, an economic justification for undertaking forest fertilization on an extensive scale requires definition as does the "optimal" limits below which such measures should be resorted to.

On the whole, there is, among the authors of the present work, a gratifying cognizance of these fundamental deficiencies in our knowledge of the need for and effects of forest fertilization. The exercise of such disciplined awareness must, of necessity, continue to be an important part of the mental equipment of all those engaged in the field for some time to come, for the long-term nature of much of the research initiated on such problems (and here reported on in detail for southern pine forests) makes it unlikely that definitive results and recommendations will be forthcoming for a number of years.

As a source of information on the mineral nutrition of trees, the present work, while valuable, cannot compare with the published proceedings of a similar symposium held at Duke University in 1958 (School of Forestry Bulletin No. 15, 1959).

It is curious that the knowledge accumulated in the last 25 years on the mineral nutrition of citrus crops, pecan, tung and other horticultural species receives no mention in the present volume.

Methods employed in the basal and foliar application of herbicides for the control of undesirable woody growth are given informative treatment in Part II. The use of aircraft in the extensive application of herbicides in the South is thoroughly covered. A short but pithy account of Mr. J. A. Kirch on the absorption, translocation and ultimate toxicity of the commoner herbicides in woody plants is as good an account of these matters as has appeared anywhere. It is followed by discussion of the necessary legal precautions that must attend the use of these chemicals.

The chemical warfare being waged on the "vicious triumvirate" — fire, insects and disease — is given an airing in Part III. Those whose interests revolve around the protection of forests will derive much encouragement from the accounts given of the relative efficiency of many of the implements in this chemical arsenal. But it is to be hoped that all of them will read the concluding and sobering article by Mr. J. L. George on the effects of widespread use of such chemicals on wildlife populations. A balanced accounting of the effects of such use has not yet been made. In terms of the greatest good and the wisest use of the resource, it may transpire that, in certain cases, the forester and his chemicals will have to stay at home.

Uniting as it does so many facets of man's involvement with the forest, this little volume is well worth the moderate sum required for its purchase. Its appeal is wider than the title would suggest. It will doubtless serve as an informative source for research workers actively involved with the use of chemicals in forest practice. — WILLIAM F. MURISON, Harvard Forest, Petersham, Massachusetts.

THE DOUBLEDAY PICTORIAL LIBRARY OF NATURE. Edited by James Fisher, Sir Julian Huxley, Sir Gerald Barry and J. Bronowski. Doubleday and Company, Garden City, New York. 1960. 359 p., illustrated. \$9.95.

All too often "nature books" attempt to amaze, astound or thrill their readers; all too few attempt to be truly informative. Even those which are factually reasonably accurate are often written with a liberal supply of exclamation

tion points and superlatives, or with the implied attribution of human emotions and motives to organisms that obviously cannot possess them. (I find it difficult for example, to believe that a pitcher plant can be guilty of treachery.) And even a well written nature book usually leaves the reader only a set of perhaps very interesting, but nevertheless mostly unrelated, facts about a miscellany of odds and ends. Except for actual textbooks and others with a similar pedantic approach, very few efforts are made to provide information about the basic phenomena that underlie all aspects of nature; an even smaller number have succeeded in doing so in a thoroughly interesting and readable manner. This volume is one of the select few.

As stated on the dust jacket, this book is "the story of our planet Earth and the life upon it." Obviously no book of 359 pages, even when provided with multitudinous pictures presumably worth ten thousand words each, can do full and complete justice to a subject of such scope. The editors have, however, exercised excellent judgment in their choice of material for inclusion, and have put together a well balanced volume. Generalizations and simplifications are never carried to the point of actually misleading the reader, as can so easily happen. The discussion of many subjects is not only accurate, but includes some of the more recent research and concepts developed by professional biologists and geologists that has not as yet found its way into many textbooks.

The style and manner of presentation are interesting and entertaining as well as informative. The many illustrations, ranging from simple line sketches to full color reproductions, are intimately woven together with the textual material. As might be expected from the list of editors and advisors, there is an indefinable, but unmistakable, British flavor, despite the careful Americanization of spellings and word usages. This, perhaps, is one of its advantages. The Europeans have, on the whole, been far more successful than Americans in popularizing scientific and scholarly subjects, making them intelligible and interesting to the lay reader without juvenilizing them. Only within the last few years have an appreciable number of American books of comparable intent and quality appeared.

In addition to the body of the text there is an appendix, though not titled as such, which includes about 25 pages devoted to a complete classification, to the ordinal level in some groups, to the class level in others, of the plant and animal kingdoms, and a glossary of about fourteen pages. Perhaps some idea of the scope and level of the book can be obtained from the fact that the "A's" in the glossary include such words as achene, adaptive radiation, allele, anaerobic, anastomosis, antibiotic, antigen, anticline, atoll and auxin.

This is the second in a series of eight projected volumes, the first having been the Doubleday Pictorial Library of Science.—J. A. TIHEN, University of Notre Dame, Notre Dame, Indiana.

MARK CATESBY, THE COLONIAL AUDUBON. By George Frick and Raymond Phineas Stearns. University of Illinois Press, Urbana. 1961. x + 137 p. Illus. \$5.00.

The British zoologist George Edwards wrote to Thomas Pennant that Catesby was "too modest to rise in the world by pushing his interest amongst the great, to many of whom he had access." This was twelve years after Catesby's death. His great folio work on the *Natural History of Carolina, Florida and the Bahama Islands*¹ was his consuming task and remains his monument.

¹ Cf. W. T. Stearn (*Jour. Soc. Bibliog. Nat. Hist.* 3:328. 1958) for dates of issue not mentioned by authors.

Elliott Coues' verdict of 1878: "classic, conspicuous in merit *inter congeneres sui temporis*, and indispensable for occasional consultation" stands today.

For his pioneer account of birds, illustrated with one hundred plates, Catesby has been designated the founder of American ornithology. As Swainson remarked, he was the first author to launch natural history books in folio on the expensive subscription plan for which Audubon and Gould are justly famous.

Pulteney published the first biographical sketch of Catesby in 1791 and it was extensively quoted until Dr. Elsa Allen published fresh materials in 1951. Since then Phineas Stearns has written in fine detail of Petiver, and recently George Frick (*Bibliog. Soc. Amer. Papers* 54:163-175, 1960) on some of the more disputed points in Catesby's life. These two professional historians, Frick of the University of Delaware and Stearns of the University of Illinois, have searched far and researched well to produce this handsome volume on Catesby the man and the naturalist, well documented, temptingly illustrated and, happily, modestly priced.

Someday Catesby's *Natural History* will be reissued, somewhat along the lines of William Vogt's edition of Audubon's *Birds of America*, if not more ambitiously. Perhaps to guide the editor of that hoped-for *redivivum* it may be germane to elaborate on some points raised in my brief review in *Science* (134:467, 1961). The most unsatisfied need in a study of Catesby now, as Elsa Allen remarked ten years ago, is to localize his movements in Virginia and Carolina toward as precise an itinerary as possible. This may have to wait for unfound manuscripts, and may indeed prove hopeless, but the plant collections he made survive, and if they were studied critically by a field botanist conversant with the habitats of the Carolina flora and an eye for those with restricted ranges, it might prove a long start in that search. The lack of any ticketed bird skins is unfortunate, but, judging from Audubon and to a lesser extent, Wilson, bird artists were not necessarily skilled birdskin preparators. Those original Catesby drawings preserved in the Royal Library at Windsor may carry some memoranda as to the time and place, or source of the materials illustrated.

Considering their period, Catesby's are good figures. There are several lapses (e.g. the heath hen with long ear tufts). Richardson, the art historian of Detroit, recently described the Catesby plates as "crudely engraved but nonetheless strong, decorative, and beautiful." The contemporary British art historian, Wilfred Blunt, is severe and accurate when he labels Catesby a "conscientious amateur." Ten of Catesby's bird plates are reproduced in black and white by Frick and Stearns.

The conchologist Guy Wilkins (1953) reported on Sir Hans Sloane's shell collection which by 1728 had reached a total of 4,911 specimens, the increase of the three previous years perhaps due to the return of Mark Catesby in 1726 from the New World. Catesby published only two terrestrial and two marine shells identified with the aid of Martin Lister's *Historia conchyliorum* which contained John Banister's Virginia contributions. Though Catesby's influence on insect taxonomy in the Linnaean period was negligible, he figured twenty-six insects, nearly half lepidopterous. In paleontology Catesby was preceded by John Banister who left descriptions of the backbone of a whale and of a number of fossil teeth, bones and shells. This was thirty-five years before Catesby described the grinders of an elephant.

There is some interest in Catesby's proposing Lieut. General James Oglethorpe as a member of the Royal Society. The authors remark on the Gen-

eral's plant collections from Georgia. In this connection it is interesting to recall that Dr. William Houstoun (d. 1733) would, had he lived, have botanized in Georgia at the instigation of Oglethorpe.

Catesby's botanical contributions were not slight. The authors treat them extensively in Chapter Six. John Martyn's sumptuous folio work, the *History of Rare Plants*, reported on Catesby's novelties in 1728, only four years after his introductions had been planted at Chelsea. Martyn's *History*, by the way, consisting of fifty color plates, described by Pritzel as "elegantissimae certe sunt," has been compared with Catesby's own *Natural History* for its grand plan. The role of Catesby's illustrations in giving graphic validity to Linnaeus's new species published in the *Species plantarum* has been given its due recognition. Linnaeus gave scant attention to the dried plants brought back by Catesby for he was chiefly engrossed with the living plants growing in the Physick Garden at Oxford.

At times Catesby was an accurate observer: he wrote that Dahoon Holly (*Ilex cassine*) was "rare, seen only on Col. Bull's Plantation on Ashley River, where it grows in a bog." The Charleston naturalist, Laura M. Bragg, confirmed its rarity. Other Catesby descriptions she found "inadequate and unscientific." Leaf venation was often conventionalized beyond use in identification. James Edward Smith remarked that the want of a sketch of flower parts was the principal defect, but that the state of botany then did not suggest this to Catesby.

Peter Collinson was apprehensive of the cost of the Catesby folios as they appeared, and so perhaps it was he who encouraged Catesby to prepare a modest summary of his observations of 85 trees. This appeared first as *Hortus Britanno-Americanus*. Though Frick and Stearns insist that this work "was finished by Catesby shortly before his death," it shows the heavy hand of the publisher. It is interesting that the *Hortus*, published in 1763, sold lamely — Joseph Banks who zealously acquired such works missed it — and that it was repackaged four years later by a second publisher, but it continued to be ignored by the general public. It was indeed the *Natural History*, with its "broad appeal," that established Catesby's position. Catesby remained the standard authority through the eighteenth century. It is significant that Peter Collinson checked Bartram's discoveries bird by bird and plant by plant with Catesby. On the William Bartram drawings acquired by Lord Derby and preserved at Knowsley Hall may often be noticed the touchstone "Not in Catesby." Winterbotham wrote a four-volume *Historical . . . view of the United States of America* in his cell in debtor's prison and he refers to Catesby in noticing the "Hooping Crane," the "Flammant or Flamingo," the "Water-frog" (*Rana catesbeiana*), and the "Land-frog." Southey is said to have passed the books through the prison windows on a kind of interlibrary loan. At this point we may wince at the weight of a set of Catesby, if not at its rarity!

Frick and Stearns reaffirm Catesby's death evidently on conclusive grounds as 1749 rather than 1750. They uncovered a letter written by George Edwards to Thomas Pennant in 1761 in which Edwards remarks upon attending Catesby's funeral. There the argument rests. Two centuries later we have an intriguing portrait of the man and his work.—JOSEPH EWAN, Tulane University, New Orleans.



